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Running head: LOCAL BIODIVERSITY CHANGE

Estimates of local biodiversity change over time stand up to scrutiny

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23 *Abstract.* We present new data and analyses revealing fundamental flaws in a critique of two
24 recent meta-analyses of local-scale temporal biodiversity change. First, the conclusion that
25 short-term time series lead to biased estimates of long-term change was based on two errors in
26 the simulations used to support it. Second, the conclusion of negative relationships between
27 temporal biodiversity change and study duration was entirely dependent on unrealistic model
28 assumptions, the use of a subset of data, and inclusion of one outlier data point in one study.
29 Third, the finding of a decline in local biodiversity, after eliminating post-disturbance studies, is
30 not robust to alternative analyses on the original dataset, and is absent in a larger, updated
31 dataset. Finally, the undebatable point – noted in both original papers – that studies in the
32 ecological literature are geographically biased, was used to cast doubt on the conclusion that,
33 outside of areas converted to croplands or asphalt, the distribution of biodiversity trends is
34 centered approximately on zero. Future studies may modify conclusions, but at present,
35 alternative conclusions based on the geographic-bias argument rely on speculation. In sum, the
36 critique raises points of uncertainty typical of all ecological studies, but does not provide an
37 evidence-based alternative interpretation.

38 *Key words: biodiversity, meta-analysis, species richness, temporal change.*

39 INTRODUCTION

40 Patterns of biodiversity over space and time represent the foundation of many ecological theories
41 and conservation prioritization schemes. Concerns have been raised (Gonzalez et al. 2016) about
42 two papers that collectively analyzed >250 individual datasets on biodiversity change through
43 time from many parts of the world (Vellend et al. 2013, Dornelas et al. 2014). Both of these
44 studies found that the average magnitude of temporal change in alpha diversity across studies
45 was indistinguishable from zero. Dornelas et al. (2014) additionally showed significant and

46 consistent temporal species turnover, thus highlighting marked shifts in community composition.
47 The concerns of Gonzalez et al., which focus on species richness and diversity, are for the most
48 part typical of those that could be directed at any ecological meta-analysis: different results
49 might obtain in different places (underrepresented regions) or times (before people collected data
50 of this nature), and it is possible to find data subsets that deviate from the overall pattern. These
51 concerns were used by Gonzalez et al. to call into question our conclusions. Some aspects of the
52 Gonzalez et al. critique relied on their selective use of data and methods of analysis, while others
53 focused on the nature of the data themselves and accompanying interpretations.

54 Here we present analyses, as well as new data, to support the following conclusions: (1) Well-
55 replicated short-term time series do not provide biased estimates of long-term biodiversity
56 trends. The opposite conclusion presented by Gonzalez et al. was based on two errors in their
57 simulation model and calculations. (2) There is no compelling evidence that studies of longer
58 temporal duration show greater biodiversity decline. On this point, the analyses presented by
59 Gonzalez et al. were contingent on a single outlier data point and to unrealistic assumptions
60 about model structure, and the results were not robust to the inclusion of additional data. (3)
61 There is no evidence in our original analyses or using a larger, updated dataset that the results
62 were biased due to combining the effects of disturbance with post-disturbance dynamics. In fact,
63 selectively excluding post-disturbance dynamics is itself a source of bias. (4) The ecological
64 literature is indeed geographically biased, a fact discussed explicitly in both Vellend et al. (2013)
65 and Dornelas et al. (2014). The analysis of Gonzalez et al. on this issue supports the undebatable
66 conclusion that new data (in this case from underrepresented regions) might modify conclusions
67 from these meta-analyses, or from any other global-scale ecological meta-analysis.

68 SHORT-TERM TIME SERIES DO NOT PROVIDE BIASED ESTIMATES OF LONG-TERM TRENDS

69 As we show below, a key component of the Gonzalez et al. critique is incorrect (i.e., not a matter
70 of selective interpretation). Simulations of species richness (S) over 50-year periods and
71 subsequent calculations of log ratios ($\log(S_{\text{after}}/S_{\text{before}})$) or slopes of richness on time during
72 shorter time intervals (5, 10, 20 years) were used to argue that “Estimates of biodiversity change
73 are systematically biased when syntheses are based on datasets composed primarily of short time
74 series”. Gonzalez et al. made two different errors, the first of which applies only to log ratios,
75 the second of which applies to both log ratios and slopes:

76 (i) When calculating a mean effect size for “short” windows of time, Gonzalez et al. did not take
77 into account the fact that a log ratio across, for example, a 10-year period is only expected
78 (mathematically) to capture one fifth of the amount of change that occurs over 50 years. In other
79 words, they did not multiply the average of 10-year windows by 5 before comparing with the 50-
80 year effect size. This is equivalent to the argument that, hypothetically, temperature only went
81 up by 0.5C per decade, so the estimate of the “real” increase of 2.5C over 50 years is biased.

82 (ii) The second problem is less obvious, but no less important, and it accounts for apparent
83 diversity increases in medium-sized time windows (e.g., 20 years) when a 50-year period shows
84 a richness decline initially, followed by an increase, and then a leveling off (see Fig. 1a-c). The
85 problem is that with a bounded range of 50 years, “randomly” chosen segments of 20 years
86 severely over-represent the middle portion of the time series. In another well-known ecological
87 context, this is called the mid-domain effect to explain peak species richness at central latitudes
88 or altitudes (Colwell and Lees 2000). However, whereas the boundaries in space are real, the
89 temporal boundaries are not, as time may be considered infinite in both directions. The first
90 point in the time series, for example, is only part of one 20-year segment in the “population”
91 from which the Gonzalez et al. simulations sample, 0:20. The second time point is part of two

92 segments, 0:20 and 1:21, and so on. Time points 20-30, on the other hand, are each part of 20
 93 different segments. So, with the decline in richness happening early during the 50-year time
 94 span, seemingly random samples of 20 years mostly miss the decline, while “detecting” a
 95 transient increase only because it happens to occur in the middle portion of the time series. The
 96 apparent bias detected by Gonzalez et al. is an artefact of their simulation analysis focusing on an
 97 arbitrary bounded time interval (Fig. 1).

98 If one examines sequential, non-overlapping portions of any length of a given time series, the
 99 average log ratio captures precisely the rate of change over the entire time series. Simulations
 100 are not required to demonstrate this point, although we provide one corrected example from
 101 Gonzalez et al. (Fig. 1), in addition to the following explanation from first principles. Imagine
 102 we have a species-richness (S) time series of five points, $t_0:t_4$, and thus four year-to-year
 103 transitions. The log ratio from beginning to end is $\log(S_4/S_0)$. The average of one-year intervals
 104 is:

$$105 = (\log(S_1/S_0) + \log(S_2/S_1) + \log(S_3/S_2) + \log(S_4/S_3)) / 4$$

$$106 = (\log(S_1) - \log(S_0) + \log(S_2) - \log(S_1) + \log(S_3) - \log(S_2) + \log(S_4) - \log(S_3)) / 4$$

$$107 = (\log(S_4) - \log(S_0))/4$$

$$108 = \log(S_4/S_0)/4$$

109 So, as long as we account for the fact that the one-year intervals cover only one quarter of the
 110 full time series (i.e., we multiply this by four), we recover the original “target” log ratio for the
 111 full time series precisely (see also Fig. 1g). The same result will hold for two-year intervals in
 112 this time series, 10-year intervals of a 50-year time series, or any other combination. The same
 113 precise mathematical equivalence does not hold for slopes, but it is equally true that there is no

114 systematic bias introduced by the fact of sampling a subset of a longer time series. An
115 incomplete sample of the portions of the longer time series will introduce variance (as is always
116 the case with sampling), but not systematic bias (Fig. 1). The conclusion, based on simulations,
117 “that short time series can provide unreliable estimates of a known trend” (Gonzalez et al. 2016)
118 is simply incorrect.

119 LOCAL BIODIVERSITY TRENDS IN STUDIES OF DIFFERENT DURATION

120 The argument that short-term time series bias estimates of temporal biodiversity trends was used
121 by Gonzalez et al. as a springboard to asking whether longer duration studies tend to show
122 biodiversity declines. In this section, we address this issue for the two original studies in turn.

123 Using the data from Vellend et al. (2013), Gonzalez et al. modeled the log ratio of species
124 richness at the end and start of a study (see previous section) as a function of the duration of that
125 study, finding a statistically significant ($p = 0.04$) but weak relationship (Fig. 2a). They
126 emphasized the conclusion that longer-duration studies tend to show richness declines, although
127 by allowing for a non-zero intercept, their results also require explaining a nonsensical positive
128 biodiversity trend in studies that last zero years. If one makes the ecologically realistic
129 assumption that the log ratio must be zero at duration = 0 (i.e., a zero intercept), not only is the
130 slope not significant, but its raw value is actually positive rather than negative (Fig. 2B). This
131 illustrates the potentially major influence of assumptions about model structure on the spurious
132 detection of weak statistical relationships.

133 Given the controversy sparked by Vellend et al. (2013), we have since expanded the data set by
134 37% to include studies published through the end of 2014 (the original paper had studies
135 published up to July 2012; see Metadata S1 for data and computer code). The methods were

136 identical to those in Vellend et al. (2013), except that we did not additionally read through the
137 references of all new papers to find additional data sets. With the larger data set of 212 studies
138 (the 2013 paper had 155), there is no significant relationship between local richness change and
139 study duration, regardless of whether one allows for a non-zero intercept (Fig. 2c,d).

140 The data in Dornelas et al. (2014) includes studies with diversity estimates for at least three time
141 points, thus allowing the estimation of slopes of diversity vs. time, rather than only before-after
142 log ratios. There is no significant relationship between the diversity-time slope and study
143 duration (Fig. 3a,b). Gonzalez et al. chose instead to calculate log ratios using the data in
144 Dornelas et al. (2014; see Dataset S1 in that paper), thereby excluding most of the data used by
145 Dornelas et al, and reported a significant negative relationship between log ratios and study
146 duration (Fig. 3c). Again their analysis allowed for a non-zero intercept; if the intercept is fixed
147 at zero – as expected after no time has elapsed – the relationship is not significant (Fig. 3d). In
148 addition, the Gonzalez et al. result is highly sensitive to one outlier, depending not just on a
149 single study (reference 90 in Dornelas et al. 2014), but on a single data point in that study
150 (species richness = 43 in 1911, and <20 for the next 90 years). In the absence of that one data
151 point, the relationship is not statistically significant, regardless of whether one assumes a zero or
152 non-zero intercept (Fig. 3e,f).

153 In sum, the evidence provided by Gonzalez et al. to support their claim that longer-duration
154 studies tend to show biodiversity decline is exceedingly weak at best. Their conclusions depend
155 on specific and unrealistic assumptions, and provide negligible predictive value. Whether using
156 the realistic assumption of zero biodiversity change at duration = 0, using a larger data set, taking
157 account of an outlier, or analyzing slopes instead of log ratios, we find no convincing evidence
158 that estimates of biodiversity change depend on study duration. In any given time series, it is

159 clearly possible (and indeed likely) that trend detection will depend on the particular period of
160 time analyzed. In our analyses, the observed trends were evenly spread above and below zero
161 for the range of durations, and well-populated with data (<50 years or so). There is thus, at
162 present, no evidence to support Gonzalez et al.'s conclusion that longer-duration studies
163 systematically show average local biodiversity declines. We recognize that all of these analyses
164 were carried out with respect to baselines determined by the beginning of the time series
165 involved. There will be cases where ecosystems have lost or gained biodiversity before these
166 observations began, but at present we cannot assess the frequency of these different scenarios.

167 EFFECTS OF DISTURBANCE

168 Another concern of Gonzalez et al. (see also Eisenhauer et al. 2016) was the simultaneous
169 inclusion of (i) studies that characterize the effects of disturbance (“impacts”) and (ii) studies that
170 characterize recovery from disturbance (“recovery”). If our goal had been to assess only the
171 direct effects of disturbance (e.g., Supp and Ernest 2014), this would indeed have been
172 inappropriate. But that was not the goal of either original paper. In a world with fire, grazing,
173 logging, and other disturbances of varying intensity and frequency, to include only the effects of
174 such disturbances and to ignore locations recovering from past disturbances constitutes the
175 introduction of a bias in itself. Gonzalez et al. pursued this line of inquiry by selecting studies
176 classified as “post-disturbance”, “post-fire”, and “cessation of grazing”, for elimination from the
177 Vellend et al. (2013) dataset (i.e., leaving the impact-only data subset).

178 Unlike the primary analyses in Vellend et al. (2013), Gonzalez et al. analyzed raw log ratios
179 rather than those expressed as change per decade, and they weighted studies by the square root of
180 sample size. The result was a distribution of effect sizes with an upper confidence limit that was
181 slightly negative (1% loss). However, this significant result depends on the combined influence

182 of the two analysis modifications introduced by Gonzalez et al. Using the original unweighted
183 analyses and only the data reported in Vellend et al. (2013), the 95% credible intervals for the
184 impact-only data subset selected by Gonzalez et al. overlap zero both for raw log ratios, if only
185 slightly ($[-0.095, 0.012]$ or between 9% loss and 1% gain), and for change expressed per decade
186 ($[-0.061, 0.031]$). More importantly, using the larger, updated dataset, the upper credible
187 intervals are well above zero (raw log ratio: $[-0.053, 0.034]$; per decade: $[-0.038, 0.032]$),
188 allowing us to reject the conclusion that eliminating “recovery” studies reveals an average
189 decline in local plant biodiversity.

190 More generally, we disagree with the argument that disturbances (anthropogenic or otherwise)
191 are generally expected to cause a decline in local biodiversity. Empirical studies testing the
192 effect of disturbance on species diversity find a wide range of results, including no effects,
193 positive effects, negative effects, and hump-shaped relationships (Mackey and Currie 2001; Supp
194 and Ernest 2014; Newbold et al. 2015; Vellend et al. 2017). Even logging – implicitly
195 emphasized in Gonzalez et al.’s analysis of forest cover change – is often followed by a short-
196 term increase in local plant diversity (due to colonization of early-successional species) and a
197 subsequent longer-term decline back to levels similar to old-growth forest (Halpern and Spies
198 1995; Duguid and Ashton 2013). In this scenario, capturing only the long-term “recovery” phase
199 would bias results against positive trends rather than negative trends. The opposite scenario (the
200 concern of Gonzalez et al.) certainly exists as well, with biodiversity potentially decreasing after
201 disturbance. Disturbance does not have a unidirectional effect with a single recovery trajectory,
202 so even if studies captured some phases of the disturbance cycle more than others, the
203 consequences would not be easily predictable.

204 In sum, both short-term and longer-term changes in local biodiversity caused by disturbance are
205 relevant to understanding temporal biodiversity trends, and the empirical data indicate highly
206 context dependent effects of disturbance on the magnitude and direction of biodiversity change.

207 THE ECOLOGICAL LITERATURE IS INDEED GEOGRAPHICALLY BIASED

208 Ecological studies of all kinds have been conducted far more often in Europe and North
209 America, and nearby waters, than elsewhere. In the case of our meta-analyses, we are unable at
210 present to estimate with confidence how local biodiversity has changed in under-recorded or
211 unrecorded regions, such parts of Africa or the Indian Ocean. This is a challenge for global
212 analysis of biodiversity change, and we hope that highlighting this challenge will instigate more
213 data collection in these regions. However, while any given subset of data might deviate slightly
214 from the overall pattern, there was no obvious signal that geographic bias led to bias against
215 finding biodiversity decline. For example, in Vellend et al. (2013), the estimated mean log ratios
216 of species richness change over time for South America (N = 12), Asia (N = 9), Australia (N =
217 5), and Africa (N = 2) were all positive. One could choose to conduct an analysis giving greater
218 weight to these understudied regions: this would shift the estimated central tendency towards
219 biodiversity increases rather than decreases. In addition, the analyses of Gonzalez et al. show
220 that one of the original meta-analyses had an underrepresentation of places with high recent
221 human impacts (Vellend et al. 2013), while the other had an *over*representation of places with
222 high human impacts (Dornelas et al. 2014), and yet both studies show a similar distribution of
223 temporal changes in local diversity.

224 Gonzalez et al. have identified some important axes along which we might improve the future
225 representativeness of biodiversity studies (e.g., regional diversity, human impacts), but
226 ultimately only new data from underrepresented regions can speak directly to what is happening

227 in those parts of the world, and thus prompt a potential re-assessment of conclusions. Local
228 biodiversity change is very much dependent on specific, local circumstances, and new and
229 interesting results from poorly known regions may well emerge in the future. Improving the
230 spatial representation of these regions is a high priority in obtaining better estimates of local
231 biodiversity change.

232 In sum, Gonzalez et al. present analyses to demonstrate a point noted in both original papers: the
233 data are geographically biased. Precisely the same limitation applies to most ecological
234 synthesis and meta-analysis papers (e.g., Cardinale et al. 2012, Hooper et al. 2012, Elahi et al.
235 2015, Haddad et al. 2015), in which there was no such vigorous effort to quantify geographic
236 bias and its attendant consequences for limiting the scope of conclusions. We are working with
237 the best data available, and continue to assemble data, to directly document temporal biodiversity
238 change at the local scale. Converting natural ecosystems to croplands or parking lots causes a
239 local loss of biodiversity (Newbold et al. 2015), but otherwise there is a great deal of variation
240 but no clear tendency for the net temporal local biodiversity trend to be different from zero
241 across the sites in the available data (Vellend et al. 2013, Dornelas et al. 2014, Elahi et al. 2015).

242 TO CONCLUDE

243 We agree with Gonzalez et al. concerning the need for better biodiversity monitoring in the
244 future. Our knowledge of a great many places on earth is quite limited, and many drivers of
245 biodiversity change are expected to push in opposite directions (Vellend et al. 2017). For
246 example, non-native species introductions typically increase regional-scale species richness (Sax
247 and Gaines 2003, Winter et al. 2009), and in areas that are currently cold and humid (e.g.,
248 temperate-zone mountain tops), species richness is also expected to increase due to climate
249 warming (Pauli et al. 2012). On the other hand, nitrogen deposition often causes plant diversity

250 to decline (Simkin et al. 2016), and for some taxa habitat fragmentation can do the same (Haddad
251 et al. 2015). How different forces balance out in the future can best be determined by systematic,
252 long-term monitoring – a major priority for future research in ecology and conservation.

253 Causes and trends of local biodiversity, and therefore any applied consequences, are just as
254 described: local. The global average across many local trends is thus of applied significance
255 only indirectly, via framing arguments about the consequences of biodiversity change (e.g.,
256 Hooper et al. 2012). Given the data at hand, we can reject the notion of local biodiversity loss as
257 the general rule, and whether new data reveal a ratio of positive vs. negative trends at 50:50,
258 60:40 (positive mean), or 40:60 (negative mean), context dependence and site-specificity would
259 remain the dominant pattern. The most generally applicable statement we can make at present is
260 that in most situations we expect substantial changes in species composition – that is, species
261 turnover – with important implications for biodiversity conservation efforts (Dornelas et al.
262 2014, Magurran 2016).

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329 **Figure captions**

330 FIG. 1. Mean \pm standard deviation of log ratios ($\log(S_{\text{after}}/S_{\text{before}})$) and slopes (species richness vs.
331 time) for repeated samples of short time series sampled from a longer (50-year) duration data set.
332 (a) A reproduction of Fig. S3D from Gonzalez et al., showing one example of species richness
333 dynamics over time that appeared to lead to especially biased results. (b,c) Results of 1000
334 seemingly random samples of different duration conducted according to the methods of
335 Gonzalez et al.; these results appear to show an average positive trend among moderate-duration
336 samples, despite a long-term negative (log ratio) or flat (slope) trend over the full duration. (d,e)
337 Log ratio results when correcting separately for duration (problem (i) in main text) and overlap
338 (problem (ii) in main text); here we see that just accounting for the duration of data subsets
339 removes bias from short-duration samples, while correcting for overlap removes any tendency
340 for positive average trends. (f) Slope results after correcting the overlap problem. (g) Log ratio
341 results after correcting for both problems; here the averages are precisely equal to the long-term
342 trend. Note that when correcting for overlap, we only use durations that are multiples of the 50-
343 year total time span.

344 FIG. 2. Relationships between local plant species richness change over time (y-axis) and the
345 duration of a study, modeled assuming either a non-zero y-intercept (a,c) or a zero y-intercept
346 (b,c), using the original data in Vellend et al. (2013) (a,b) or an expanded dataset (c,d; new data
347 points shown in red). The effect size for temporal richness change is expressed as the log ratio
348 of species richness in the final year of study (SR_2) and in the initial year of study (SR_1). Lines
349 represent the estimated effect size with credible intervals. See Appendix S1 for statistical
350 methods and Metadata S1 for all data and computer code.

351 FIG. 3. Relationships between species richness change over time (y-axis) and the duration of a
352 study, using data from Dornelas et al. (2014). Relationships were modeled assuming either a
353 non-zero y-intercept (a,c,e) or a zero y-intercept (b,e,f), using either slopes (a,b) or log ratios (c-
354 f) to express temporal biodiversity change, and either including one outlier (a-d, “Original
355 dataset”) or not (e,f, “Modified dataset”). Lines represent the estimated effect size with credible
356 intervals. See Appendix S1 for statistical methods and Metadata S1 for all data and computer
357 code.