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6     ESTIMATING LOCAL BIODIVERSITY CHANGE:  A CRITIQUE OF PAPERS CLAIMING

7     NO NET LOSS OF LOCAL DIVERSITY

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31   *Abstract:* Global species extinction rates are orders of magnitude above the background rate

32   documented in the fossil record. However, recent data syntheses have found mixed evidence for

33   patterns of net species loss at local spatial scales. For example, two recent data meta-analyses

34   have found that species richness is decreasing in some locations and is increasing in others.

35   When these trends are combined, these papers argued there has been no net change in species

36   richness, and suggested this pattern is globally representative of biodiversity change at local

37   scales. Here we re-analyze results of these data syntheses and outline why this conclusion is

38   unfounded. First, we show the datasets collated for these syntheses are spatially biased and not

39   representative of the spatial distribution of species richness or the distribution of many primary

40   drivers of biodiversity change.  This casts doubt that their results are representative of global

41   patterns. Second, we argue that detecting the trend in local species richness is very difficult with

42   short time series and can lead to biased estimates of change. Re-analyses of the data detected a

43   signal of study duration on biodiversity change, indicating net biodiversity loss is most apparent

44   in studies of longer duration. Third, estimates of species richness change can be biased if species

45   gains during post-disturbance recovery are included without also including species losses that

46   occurred during the disturbance. Net species gains or losses should be assessed with respect to

47   common baselines or reference communities. Ultimately, we need a globally coordinated effort

48   to monitor biodiversity so that we can estimate and attribute human impacts as causes of

49   biodiversity change. A combination of technologies will be needed to produce regularly updated

50   global datasets of local biodiversity change to guide future policy.  At this time the conclusion

51   that there is no net change in local species richness is not the consensus state of knowledge.

52   *Keywords*: Anthropocene, biodiversity monitoring, species richness, meta-analysis, extinction,

53   invasion, time series, baselines

54   INTRODUCTION

55   Humans are affecting the abundance and distribution of species across the planet, and these

56   impacts are projected to increase in the 21$^{st}$ century (Pereira et al. 2010, Pimm et al. 2014). As

57   much as 50% of the Earth's ice-free land surface has been transformed into agriculture and urban

58   land cover (Ellis and Ramankutty 2008), one third of all forest has been cleared and most of the

59   rest is fragmented (Haddad et al. 2015), the ocean is heavily impacted (Halpern et al. 2008), and

60   virtually all land has been affected by pollution and climate change.  Since 1600, an estimated

61   906 known species have gone extinct globally (IUCN 2015).  While this represents a small

62 fraction of the world's eight or more million species of eukaryotes (Mora et al. 2011), the rate of
63 extinction (>900 species in ca. 400 years) is 100-1000 times the historical rate in the fossil record
64 (Pimm et al. 2014, Ceballos et al. 2015). Moreover, more than 20,000 species are now
65 threatened with extinction - a number that has doubled since 2000 (IUCN 2015). Uncertainty
66 exists about the rate of global extinction due to incomplete sampling and identification of most
67 of the remaining biodiversity on Earth (Regnier et al. 2015), the time lag between human impacts
68 and extinction (Gilbert and Levine 2013, Essl et al. 2015a), and the extent to which extinctions
69 might be offset by speciation (Thomas 2013). Even so, consensus has emerged that Earth is in
70 the midst of an exceptional global extinction event that is unprecedented in the history of human
71 life (Pereira et al. 2010, Pimm et al. 2014, Ceballos et al. 2015, Regnier et al. 2015.)

72      Despite the consensus that we are losing species at the global scale, there is an emerging
73 and important debate about how biodiversity is changing at any particular location on the planet
74 where the spatial grain is typically less <1 km$^2$. Many previous studies of biodiversity change
75 have used spatial grains much larger than 1 km$^2$. The prevailing view is that human activities are
76 increasing rates of local extinction (Davies et al. 2006), and that the cumulative effect of
77 increased local extinction rates is responsible for global trends. Indirect inferences about global
78 trends in biodiversity at local scales are derived from estimates of change based on relationships
79 between suitable habitat area and endemic diversity (e.g. Jetz et al. 2007). These estimates
80 predict that endemic species richness will decline as a power function of habitat area and
81 fragmentation (e.g. Hanski et al. 2013), or shifts in suitable climate niche (Burrows et al. 2014).
82 Direct evidence for local biodiversity loss comes from syntheses of site-based studies where
83 variation in species richness is explained by a gradient of human impact (e.g., urbanization,
84 pollution, and agricultural expansion), while controlling for endemic levels of variation. This
85 method shows that these human drivers can reduce species richness at local scales (Pautasso
86 2007, McKinney 2008, Aronson et al. 2014, Newbold et al. 2015). An alternative approach
87 avoids a space for time substitution and estimates the temporal trends in species richness across
88 gradients of human impact and spatial scales (e.g., Harrison et al. 2015).

89      Alongside evidence of local biodiversity loss, however, a number of papers have shown
90 that human impacts can also increase diversity at sub-global scales (Stohlgren et al. 1999, Sax et
91 al., 2002, McKinney 2008, Ellis et al. 2012, Elahi et al. 2015). The success of some species in
92 human-dominated landscapes (Aronson et al. 2014), increases in local diversity due to

93    disturbance (DeVictor and Robert 2009), and the spread of exotic species (e.g., Bruno et al.
94    2004) are all examples. When these additions match or outpace the rate of local species
95    extinctions, then diversity in any particular location can stay the same (Byrnes et al. 2007),
96    increase (Sax et al. 2002, Elahi et al. 2015), or show high rates of species turnover (Dornelas et
97    al. 2014).

98        While there is growing recognition that human activities may either increase or decrease
99    local biodiversity, the data have generally been insufficient to quantify long-term trends in
100    biodiversity change at local scales throughout the world, and to reconcile them with global
101    estimates of species loss. To address this data gap, several recent studies have collated datasets
102    that provide direct estimates of biodiversity change through time at local scales (e.g., Vellend et
103    al. 2013, Hudson et al. 2014, Dornelas et al. 2014, Elahi et al. 2015, Newbold et al. 2015).
104    Among these, two data syntheses have reached the conclusion that there is no evidence for
105    systematic declines in species richness at local scales and claimed that their conclusions are
106    globally representative of what is happening to species richness at local spatial scales (Vellend et
107    al. 2013, Dornelas et al. 2014). Here we challenge the conclusions of these two syntheses on
108    three grounds: (1) we present new analyses showing the datasets assembled for these syntheses
109    exhibit extreme spatial bias, and are not globally representative of species richness or human
110    impacts on ecosystems that influence biodiversity; (2) we re-analyze these data and detect a
111    signal of study duration on biodiversity change, indicating net biodiversity loss is most apparent
112    in studies of longer duration. Ancillary simulations show that trends estimated with short time
113    series can be biased and lack statistical power to detect a trend; (3) we show why a lack of
114    appropriate historical baselines or spatial references precludes these studies from accurately
115    characterizing species richness change due to humans.  After laying out our critique, we reflect
116    on some lessons learned from these syntheses, and describe new challenges in accurately
117    quantifying changes in biodiversity on this planet.

118

119    THREE ESSENTIAL CONSIDERATIONS IN ASSESSMENTS OF LOCAL BIODIVERSITY
120    CHANGE

121    The synthesis completed by Vellend et al. (2013) focused on patterns of biodiversity change in
122    terrestrial vascular plants, and claimed to be *"a systematic global meta-analysis of plant species*
123    *diversity change over time in >16,000 plots from all major vegetation types, including areas*

124 *under profound and direct human influence."* Data used for this synthesis came from 346
125 existing studies that had monitored >16,000 non-experimental, 'local-scale' vegetation plots for
126 anywhere between 5 and 261 years. Vellend et al. (2013) summarized these time-series by
127 calculating log response ratios (LRR) that quantified the proportional change in plant species
128 richness from the initial to final year of the study, and divided LRR by the number of decades to
129 arrive at a proportional rate of species loss. The synthesis completed by Dornelas et al. (2014)
130 collated data from scientific papers and publicly available databases that: (1) had time-series of >
131 3 years, (2) used consistent sampling methodology, and (3) reported abundance estimates for all
132 species in samples. Their final dataset was comprised of 100 time-series representing 35,613
133 species of mammals, birds, fishes, invertebrates, and plants measured at sites and along marine
134 transects including 430,324 latitude and longitude coordinates. Although the synthesis claimed
135 to cover marine, freshwater, and terrestrial systems, the vast majority of data points included in
136 Dornelas et al. (2014) were from marine systems, primarily from cruises that had monitored
137 plankton, or from seabird, fish, and cetacean monitoring programs. In this section we raise three
138 criticisms of these two data syntheses that call into questions their primary conclusions about
139 local change in species richness.

140

141 *1. Existing time-series of biodiversity are a spatially biased representation of Earth's diversity,*
142 *and the anthropogenic drivers that cause diversity change.*

143   The datasets collated by Vellend et al. (2013) and Dornelas et al. (2014) included a large
144 number of observations taken from many locations around the globe over multiple decades.
145 However, as is true for most syntheses of existing data, they represented an opportunistic
146 collection of studies that were designed for a wide variety of purposes. The choice of which
147 studies to include in these syntheses was not guided by a geographically explicit sampling design.
148 The authors assembled any and all time-series they could find that matched their search criteria
149 in which someone, somewhere, had repeated measures of species richness at the same site for
150 any purpose. The key question in this case is whether the data collated for these syntheses are
151 sufficiently representative of the global distribution of species richness or human impacts on
152 ecosystems such that they are broadly representative of what is happening locally to species
153 richness around the globe.

154    To assess how well the Vellend et al. (2013) and Dornelas et al. (2014) syntheses capture
155    a globally representative sample of species richness and human impacts on ecosystems, we
156    quantified spatial bias in these datasets.  We began by locating existing maps of species richness
157    and human impacts on ecosystems that represent the most spatially resolved information
158    available at a global scale (see Fig. 1, and Table S1 in Supplemental Material).  For marine
159    biodiversity, we used the United Nations Environmental Programme World Conservation
160    Monitoring Centre's map of global marine biodiversity (Tittensor et al. 2010).  For terrestrial
161    plant biodiversity, we used the global map of vascular plant species richness published by Kreft
162    and Jetz (2007, their Fig. 3d).  For human impacts on the oceans, we used the Halpern et al.
163    (2008) global map of human impacts on marine ecosystems, which tallies the number of
164    anthropogenic stressors being imposed on oceans as a metric of cumulative impact.  For human
165    impacts on land, we used the Hansen Forest Cover Change dataset, which has utilized Landsat
166    images since 2000 to quantify the extent and conversion of forested habitats globally (Hansen et
167    al. 2013).  In addition to forest cover change, we compared the Vellend et al. (2013) dataset to
168    the HYDE 3.1 database (Goldewijk et al. 2010) that quantifies conversion of Earth's land surface
169    to agricultural or pastoral habitat, and a map of the Human Global Influence Index (Goldewijk et
170    al. 2010) that quantifies human built infrastructure like cities and roads.  It is important to be
171    clear that none of these maps of human impact on the world's terrestrial or marine environments
172    were specifically designed to quantify impacts on biodiversity *per se*.  As such, conclusions
173    drawn from these maps are only as good as the assumption that they accurately portray human
174    impacts on biodiversity.  Nevertheless, we use these maps because they are presently some of the
175    most comprehensive, and spatially-resolved approximations of human stressors being imposed
176    on the world's ecosystems.

177    For each of the terrestrial and marine maps used in our analysis (see Fig. 1), we randomly
178    sampled $N$ locations across the globe, where $N$ was equal to the number of sites that were
179    collated for use in the Vellend et al. (2013) synthesis (or 10,000 points for the Dornelas et al.
180    (2014) synthesis: see Supplemental Material for justification).  For each random sample of $N$
181    locations, we quantified the amount of spatial bias in those locations using Hellinger's distance $d$
182    (Schmill et al. 2014, supplemental material).  As $N$ becomes increasingly large and approaches
183    the sampling of every location $L$ (a pixel on a map), there is no spatial bias in a sample and $d$
184    becomes zero because the map has been exhaustively sampled.  However, because $N$ is always

185  less than *L*, even a random sampling of *N* points will have some spatial bias associated with that
186  sample.  By performing this random sampling effort 1000 times for each map, we generated
187  expected distributions that represent the amount of spatial bias one would expect to occur for a
188  sample composed of *N* studies, but where those studies were chosen in an unbiased manner, with
189  regard to species richness or human impact across space (further details of the analyses are given
190  in Supplemental Material).  Any random, spatially representative sample of Earth's diversity, or
191  of human impacts on Earth's ecosystems, should fall within these expected distributions (Fig. 1).
192  The studies collated for both the Vellend et al. (2013) and Dornelas et al. (2014)
193  syntheses fell well outside the distributions generated from representative sampling, with values
194  of Hellinger's *d* that were indicative of extreme spatial biases (Fig. 1).  The collection of studies
195  collated by Vellend et al. (2013) was eight standard deviations outside the mean of a spatially
196  representative sample of terrestrial vascular plant richness, and 12 standard deviations from the
197  mean of a representative sample of forest cover change.  Comparison of the Vellend et al. (2013)
198  dataset to global maps of land converted to cropland/pasture habitat, or converted to human
199  infrastructure similarly revealed biases ranging from 18 to 27 standard deviations from a
200  representative sample (see Supplemental Material, Fig. S1).  The causes of these spatial biases
201  are obvious from looking at a kernel density map showing the geographic concentration of
202  studies included in the Vellend et al. (2013) synthesis (Fig. 2a).  The vast majority of studies
203  included in the Vellend et al. (2013) synthesis were performed in the United States and the
204  European Union – a set of developed countries that have historically had stronger than average
205  financial support for biological and environmental science programs.  Given the predominance
206  of data from these two regions of the globe, temperate forests, temperate grasslands, and
207  Mediterranean forests and woodlands were over-represented by as much as $e^{1.60} = 5$ times their
208  proportional area of Earth's terrestrial land surface relative to all other terrestrial vegetated
209  habitats (Fig. 2b).  In contrast, tropical biomes that harbor the greatest terrestrial biodiversity, but
210  where monitoring programs are rare, were under-represented by as much as $e^{-2.46} = 0.09$ times
211  their proportional area of Earth's terrestrial land surface (Fig. 2b).  Boreal forests, deserts, and
212  tundra were also under-represented.
213  Studies collated for the Vellend et al. (2013) synthesis also under-represented areas of the
214  planet that have been most heavily impacted by humans through forest clear-cutting (Fig. 2c).
215  The 'loss' category from the Hansen forest cover change map was under-represented by $e^{-0.47} =$

216    0.6 times of the areal representation on Earth, of which, 32% occurs in the tropics where Vellend

217    et al. (2013) had little data.  In contrast, the Vellend et al. (2013) synthesis over-represented areas

218    where forests are now recovering after logging or natural disaster by $e^{0.52} = 1.7$ times the areal

219    coverage of these habitats (Fig. 2C, gain), and over-represented the loss-and-gain category that

220    generally describes areas of high-intensity, short-cycle forestry (Hansen et al. 2013).  This latter

221    category (loss + gain), which is common in the southeastern United States, represents only

222    0.14% of the total land area on the planet; yet the number of pixels in this category within the

223    Vellend et al. (2013) dataset was 3.7 times greater than a representative sample.

224           The potential implications of these spatial biases for estimating changes in biodiversity

225    are made more obvious by taking a closer look at a particular case study.  The inset in Fig. 2a

226    shows the location of Dalby Söderskog National Park in Sweden, which represents a 0.36

227    km$^2$ forest fragment in a landscape where nearly all of the historical forest has been converted to

228    agricultural or urban cover.  The time-series included in the Vellend et al. synthesis was from a

229    study that had documented a loss of ~3 species in this forest fragment over a period of 69 years.

230    Vellend et al. (2013) explicitly excluded from their study any sites with direct land-use

231    conversion such as clear-cutting and conversion to urban and agricultural habitat, arguing that in

232    such cases "any effect of a change in the number of species on ecosystem function will be

233    negligible compared with the effects of other changes…[on ecosystem function]" (Vellend et al.

234    2013). However, failure to consider diversity change in the majority of a landscape where most

235    of the habitat has been destroyed invalidates one of the main conclusions of this synthesis: that

236    plant biodiversity is not generally declining at local spatial scales.

237           The data collated for the Dornelas et al. (2014) synthesis were even more spatially biased,

238    lying 41 standard deviations outside the mean of a spatially representative sample of marine

239    species richness, and 32 standard deviations from the mean of a representative sample of human

240    impacts on the world's oceans.  Although the Dornelas et al. (2014) synthesis was based on

241    samples taken at >430,000 latitude-longitude coordinates, a kernel density map of geographic

242    locations shows that the vast majority of sampling sites stemmed from cruises in the Northern

243    Atlantic ocean along the coasts of the United States and Europe and, to a lesser extent, from

244    cruises departing from Australia to study the Antarctic shelf (Fig. 2d).  As a result, the North

245    Atlantic was over-represented in the dataset by $e^{-1.55} = 4.7$ times (Fig. 2e). In contrast, there was

246    little representation of data from the North or South Pacific, the Indian Ocean, or the Arctic

247    Ocean, all of which were represented by 50% less than they should have been given their

248    proportional surface area of the planet.  Thus, the Dornelas et al. (2014) dataset was only

249    representative of one of the world's major oceans, and had almost no data from those areas that

250    rank among the most diverse marine habitats on Earth (e.g., the Indo-Pacific and Indian oceans).

251    The Dornelas et al. (2014) dataset did, however, over-represent marine habitats where Halpern et

252    al. (2008) suggest the cumulative number of anthropogenic stressors is the highest.  This

253    representation is perhaps not unexpected given the preponderance of sampling sites along the

254    coastal U.S. and Europe where human impacts on marine ecosystems are most well documented.

255    The lack of a decline in richness despite heavy representation from impacted areas is interesting

256    and unexpected. Potential reasons for local increases include species invasions, recovery from

257    historical overfishing, indirect effects of overfishing on lower trophic levels, or climate warming.

258    Thus a more in depth investigation of these individual drivers, rather than just a cumulative

259    impact score, is warranted.

260           Our analyses show that the datasets collated and analyzed by Vellend et al. (2013) and

261    Dornelas et al. (2014) are not spatially representative of species diversity or human impacts on

262    land or in the oceans.  The extreme spatial bias of these datasets means that the inferences

263    Vellend et al. (2013) and Dornelas et al. (2014) made from their data to the rest of the globe are

264    unfounded (EPA 2002).  Their conclusions are limited to a select subset of well-studied locations

265    on the planet, namely the U.S., Europe and, to a lesser extent, the Antarctic shelf.  Furthermore,

266    for both data syntheses, the authors assembled data that under represent areas of the planet that

267    are undergoing major land use transitions (e.g., current deforestation, conversion to agricultural

268    or urban habitats, loss of coral reefs). Finally, for the Vellend et al. (2013) synthesis, terrestrial

269    habitats that are in recovery from past deforestation or managed for timber harvest followed by

270    succession are highly over-represented.  This suggests their conclusions may be more

271    representative of the accrual of species in successional or recovering ecosystems, than of the loss

272    species resulting from human impacts on the original system.

273    *2. Estimates of biodiversity change are systematically biased when syntheses are based on*

274    *datasets composed primarily of short time series.*

275    Vellend et al. (2013) and Dornelas et al. (2014) found no average trend in local biodiversity

276    when time series were pooled from many geographical regions, ecosystem types and taxonomic

277    groups. However, short time series have low power to detect a trend and can produce biased

278    estimates of the trend itself if the time series are nonlinear and non-stationary (Bence 1995,
279    Peters et al. 2008, Mengersen et al. 2013). In Supporting Information, we show through
280    simulation that LRR (used by Vellend et al. 2013) and regression (used by Dornelas et al. 2014)
281    on short time series inadequately estimate a known trend of declining richness (Fig. S2 and S3).
282    Crucially, we show that meta-analytic datasets dominated by short time-series have potential to
283    bias conclusions, and longer duration time series provide the most reliable estimates of the
284    known underlying temporal trend in biodiversity.  These results lead us to re-analyze the data of
285    both Vellend et al. and Dornelas et al. to look at how their conclusions may have been influenced
286    by the duration of the studies they collated.

287    *Re-analysis of the effect of duration*
288    Vellend et al. (2013) and Dornelas et al. (2014) considered the importance of study duration in
289    their analyses, but both concluded that study duration had no effect on mean local biodiversity
290    change, even though the datasets contained few time series greater than 50-years. Vellend et al.
291    (2013) calculated a rate of biodiversity change by dividing the effect size by duration (Effect
292    Size = $\ln(SRt2/SRt1)/\text{duration}$). Including duration in the denominator, rather than as a covariate
293    of the log ratio can reduce the power to detect an effect. To re-evaluate the possibility that longer
294    duration time series are more likely to reveal trends in species diversity, we reanalyzed data in
295    Vellend et al. (2013) and Dornelas et al. (2014) with linear mixed models using study duration as
296    a predictor of local biodiversity change.  Biodiversity change was measured as the log ratio of
297    species richness at the end versus beginning of each data set (Effect Size = $\ln(SR_{t2}/SR_{t1})$),
298    consistent with Vellend et al (2013) because only first and last estimates are available. We used
299    duration (number of years of the study) so that our estimates of the duration coefficient would be
300    directly comparable to the results of the models in Vellend et al. (2013) and Dornelas et al.
301    (2014). Evaluation of residuals and leverage suggested no need to log transform duration. For the
302    Vellend et al. data a linear mixed model with a random effect of duration (slope) and intercept
303    revealed a negative relation between biodiversity change and time series duration (Fig. 3a; slope
304    = -0.004 se = 0.002, P = 0.04) with 4% species loss observed after 10 years, and an average 17%
305    loss after 50 years. Analysis of the Dornelas et al (2014) data using log ratios (rather than fitting
306    a linear regression, as done originally) reveals a stronger negative relationship between
307    biodiversity change and study duration (Fig. 3b; slope = -0.01 se = 0.005, P = 0.01, reflecting, on
308    average, a decline of 10% after 10 years and 40% loss after 50 years. In our re-analysis, this

309   relationship is sensitive to the inclusion of its longest datasets, potentially reflecting a drawback

310   of using the log-ratio approach to detect change. The net effect of incorporating study duration

311   into an analysis of richness change in these data sets suggests that species richness may, on

312   average, be declining, with 4-10% loss after 10 years and 18-40% loss after 50 years.

313       Why should longer time series suggest systematic diversity loss while shorter studies do not?

314   In addition to the statistical issues outlined above, one potential biological reason that species

315   loss may only be detected in multi-decade time-series is that local extinctions can be delayed and

316   occur very slowly especially in remnant ecosystems experiencing the legacies of direct and

317   indirect human impacts (Essl et al. 2015b; Haddad et al. 2015). Because of extinction lags, short

318   duration surveys are unlikely to reveal a signal of loss against a background of local colonization

319   and extinction events, if the survey occurred before the extinction debts have been realized. In

320   fact, empirical analyses of extinction debts have shown that they may take more than a century to

321   detect (e.g., Dullinger et al. 2013, Gilbert and Levine 2013, Essl et al. 2015b). We suggest,

322   therefore, that study duration should be an important feature of study design for the estimation of

323   local biodiversity loss in future meta-analyses. More data, especially longer time series, are

324   required to reveal trends that are hidden because they occur slowly or because there is a time lag

325   years after their causes (Magnuson 1990).

326

327   *3. Estimates of biodiversity change can be biased if species gains during post-disturbance*

328   *recovery are included without also including species losses that occurred during the disturbance.*

329   *Net species change should be assessed with respect to a historical baseline or spatial reference*

330   *communities.*

331   Recent meta-analyses have inconsistent results partly because changes in biodiversity have been

332   defined and measured against different baselines. In earlier studies finding that anthropogenic

333   disturbances tend to decrease local biodiversity (Benayas et al. 2009; Jones & Schmitz 2009;

334   Murphy & Romanuk 2013), changes in biodiversity were measured against a common baseline:

335   levels of local biodiversity observed in intact ecosystems, with minimal human disturbance. In

336   contrast, recent meta-analyses of time series (Vellend et al. 2013; Dornelas et al. 2014, Elahi et al

337   2015) have measured changes in biodiversity against levels of local biodiversity observed at

338   earlier points in time, when ecosystems might have been more or less disturbed by people than

339   during recent observations. These two approaches will yield not only quantitatively different

340   results, but also qualitatively different results; net species losses measured against a mostly
341   undisturbed baseline can appear as species gains when measured against a highly disturbed
342   baseline. Consider the case where a disturbance causes biodiversity loss, and then relaxation of
343   this disturbance results in recovery of biodiversity, as observed in hundreds of previous studies
344   (Fig. 4; Benayas et al. 2009, Jones & Schmitz 2009). The former approach, which uses remnant
345   ecosystems as a spatial reference site (Fig 4b), would only conclude the recovery to result in net
346   species gains if there are more species gains during recovery than there were species losses
347   during the disturbance. In contrast, the latter approach (Fig 4c) would see all species gains that
348   occurred during recovery as net species gains if the time series started after the disturbance
349   occurred.

350       The syntheses by Vellend et al. (2013) mixed studies where biodiversity was recovering from
351   a recent disturbance (e.g., recovery of diversity on Mount St. Helens after a volcanic eruption)
352   with longer time series documenting how biodiversity changes in response to a human
353   perturbation. For example, Vellend et al. (2013) combined studies of the immediate response of
354   biodiversity to disturbance by fire, grazing, and other forms of disturbance, with studies of long-
355   term biodiversity recovery from disturbance by the same factors. We re-analyzed the responses
356   to disturbance in Vellend et al. (2013) to assess this effect (Fig. 5). With all studies included
357   (those focused on both impacts and recovery), results were consistent with the original paper
358   showing no net change in local richness ($\pm$ 95% CI, t = 0.19, P = 0.85). However, when we
359   eliminated categories of 'post-disturbance', 'post-fire', and 'cessation of grazing', the
360   distribution of effect sizes was significantly negative (t = -2.15, P = 0.03) with a 95% confidence
361   interval of $e^{-0.12}$ to $e^{-0.005}$ (1-11% species loss), and comparable in magnitude to other meta-
362   analyses of local diversity change focused on impact (Newbold et al. 2015). It is noteworthy that
363   species richness was also dependent on the duration of the driver impact, with richness declining
364   by an additional 5% decade$^{-1}$ (t = -3.19, P < 0.01). Dornelas et al. (2014) only had a few
365   terrestrial studies in their dataset, but for these, they reported a significant increase in terrestrial
366   plant diversity over time. However, monotonic increases in plant diversity were obtained from a
367   single study, where plant species richness is in succession after deforestation (Isbell et al. 2015).
368   Dornelas et al. (2014) did not provide information on which marine time series were taken from
369   sites where biodiversity was recovering from recent disturbance.  Re-analysis of this question in
370   the future would be valuable.

371

DISCUSSION

Vellend et al. (2013) and Dornelas et al. (2014) find evidence that local diversity is showing increasing and decreasing trends through time at many sites around the world. In this paper we have critiqued the conclusion that globally there is no net loss of local species richness. We have argued that this claim is unfounded for at least three reasons. First, both syntheses were based on collations of studies that exhibit substantial spatial bias in their geographic locations, and are representative of neither patterns of biodiversity variation across the planet, nor of variation in degrees of human impact on ecosystems. Second, the datasets used in both syntheses are composed of predominantly short time series that are inadequate for reliably estimating changes in biodiversity through time (see point three below). Our re-analyses of these datasets showed that longer monitoring programs are more likely to find species loss, which is consistent with our understanding that biodiversity loss can unfold over decades (Tilman et al. 1994, Essl et al. 2015a). Third, data syntheses that mix data from communities that are responding to disturbance with those recovering from a disturbance require adequate baselines, and, ideally, reference sites, to make robust conclusions about net biodiversity change due to humans. Neither synthesis considered appropriate baselines or reference sites for diversity change. We echo recent calls for greater care when conducting meta-analysis (Whittaker 2010). Biodiversity data are relatively easy to acquire from the literature but conclusions from meta-analyses are only as sound as the comparisons that are made. Our analyses suggest that neither synthesis provides sufficiently reliable information to establish globally how much local biodiversity has changed through time in the context of human activities.

Aside from our own criticisms of Vellend et al. (2013) and Dornelas et al. (2014), we have pointed out that their conclusions of no net loss of species richness at local scales lie at odds with conclusions reached by other recent data syntheses. Newbold et al. (2015) quantified changes in biodiversity in 380 datasets that allowed an impacted habitat to be explicitly compared with a spatial reference that served as a control. These authors found that on average 76% of species have been lost in the worst affected terrestrial habitats on Earth, and an average 14% have been lost across all habitats for which data are available. Murphy and Romanuk (2013) performed an independent meta-analysis that compared species richness in 327 heavily disturbed to less disturbed habitats and found that human-mediated disturbances have reduced native species

402 richness by an average 18%. Pautasso (2007) found the correlation between human population
403 size and plant and animal species richness varied between -0.90 and +0.90, with an average
404 correlation near zero (+0.08). However, Pautasso (2007) went on to show that the correlation
405 was systematically negative for local scales (study grains < 1-km, and study extents < 10 000
406 $km^2$), consistent with human-induced losses of biodiversity at local scales. While these other
407 data syntheses have their own limitations (e.g. use generic measures of impact, ignore climate
408 change, count native species only), they present a very different picture of how biodiversity is
409 changing at the local scale than did Vellend et al. (2013) or Dornelas et al. (2014).

410 Despite these conflicting results and past criticisms (Cardinale 2014, Isbell et al. 2015),
411 McGill et al. (2015) recently claimed: "There is considerable empirical evidence that continental
412 biodiversity at regional or local scales is also holding steady or increasing … recent analyses that
413 collectively assembled published data from hundreds of biodiversity inventory studies found that
414 local diversity is, on average, constant." This statement does not reflect the balance of evidence
415 on local biodiversity change in the Anthropocene, and is one side of a debate that not only has
416 yet to be resolved, but which has the potential to influence the support of policy-makers for
417 conservation, strategies used by managers to preserve or restore biodiversity, and the priorities
418 set by funding agencies and journals. Because the conservation stakes of this debate are high, we
419 would like to highlight three lessons that we have taken from recent attempts to quantify
420 biodiversity change.

421 *A Caution* – One important lesson from the controversy surrounding recent syntheses and how
422 the finding of no net change has been interpreted is that care must be taken to uphold the long-
423 held scientific value of not extending conclusions beyond what can be robustly supported by data.
424 At this time, the balance of data and scientific understanding of biodiversity change in recent
425 decades do not support a conclusion of no net change in biodiversity. We are concerned that the
426 reported conclusions to that effect could be misconstrued in the context of conservation policies
427 when, as we argue here, the evidence is not sufficiently convincing to generate a majority view
428 among experts in the field.

429 A striking example of overextending conclusions from meta-analysis is apparent in
430 Vellend et al. (2013), who framed their paper as a critique of biodiversity and ecosystem
431 functioning research. Their finding of no net change in local diversity was used to argue that "*the*
432 *clear lack of any general tendency for plant biodiversity to decline at small scales in nature*

433 *directly contradicts the key assumption linking experimental results to ecosystem function as a*
434 *motivation for biodiversity conservation in nature*" (Vellend et al. 2013). This argument is
435 illogical, however, because it confuses variables and spatial scales. Vellend et al. (2013) pooled
436 studies of changing species richness (variable Y) across a disparate set of sites and taxonomic
437 groups that underwent gains and losses in local biodiversity due to opposing processes (variables
438 $X_i$); decreases in biodiversity following perturbations (e.g. fires, grazing, volcanic eruption) and
439 increases in biodiversity as communities were recovering from perturbations. First, finding no
440 average change over these times series is not evidence that local biodiversity change does not
441 affect a third local variable (Z)—ecosystem functioning—which was not measured or included in
442 their dataset. Second, it is not the global average of these changes that matter for many
443 ecosystem properties, which are driven by the species present in the local communities. BEF
444 experiments control levels of species richness because they change locally for many reasons
445 (Wardle et al. 2011) – as is clear from the distribution of response ratios in the Vellend et al.
446 (2013) dataset.

447 Unequivocal inference about the cause of biodiversity changes requires experiments that
448 control the degree of human impact (e.g. Haddad et al. 2015). The meta-analyses of Vellend et al.
449 (2013) and Dornelas et al. (2014) did not include data from controlled experiments. Whole-
450 ecosystem manipulations with Before-After Control-Impact (BACI) analyses and their
451 extensions (Underwood 1994) are designed to deal with the difficulties of detecting change and
452 attributing the cause of change when short time-series are obtained from unreplicated systems.
453 Rather than ignore experimental evidence, it should be an essential part of meta-analytic
454 approaches to defining the expectations for the sign and magnitude of local biodiversity change.

455 Studies quantifying biodiversity change must consider alternate explanations and
456 acknowledge the limitations of analyses and datasets (e.g., spatial biases, statistical power) as
457 they pertain to the conclusions drawn. This critical scientific exchange can be difficult to
458 accomplish, particularly in general science journals where space is limited. Even so, the potential
459 legacies of scientific conclusions for public beliefs and conservation-related political decisions
460 impart an additional pressure on researchers' presentation of their findings (Mouquet et al. 2015),
461 particularly for controversial topics where data are incomplete, debate is ongoing, and the
462 balance of evidence is not yet clear.

463

464   *A Need* - Second, our re-analysis of the Vellend et al. (2013) and Dornelas et al. (2014) syntheses
465   suggests that, even though we have an abundance of time-series data, this collection of datasets
466   is inadequate to robustly support inferences about temporal changes in global biodiversity. To a
467   large extent, existing global monitoring of biodiversity change is not coordinated and does not
468   track and monitor biodiversity in a manner that is representative of where biodiversity is located
469   on the planet. Long-term and spatially extensive monitoring exists for certain species groups
470   (e.g. birds and butterflies) in wealthy countries. But, in many cases these monitoring programs
471   were not designed to evaluate human impacts on local biodiversity change. The data used in
472   recent meta-analyses were collected for a number of reasons by biologists surveying coastlines,
473   forests or grasslands, and often in systems recovering from natural or human disturbances. We
474   also lack regularly updated spatial data of cumulative impacts of humans on ecosystems

475       Biodiversity is a fundamental property of the planet's ecosystems and should be
476   systematically monitored. To do this, monitoring programs need to be spatially and temporally
477   representative across the globe (Scholes et al. 2008). The first step towards this goal would be to
478   complete a formal 'gap analysis', which would probably identify what most of us already
479   recognize, and which we present here – we need monitoring programs that extend beyond the
480   borders of the U.S. and Europe, and that capture biomes that are strongly underrepresented in
481   current biodiversity datasets, such as the tropics, boreal forests, the tundra, and deserts on land,
482   the ocean benthos, and the Indian Ocean and Indo-Pacific Oceans, which harbor large fractions
483   of marine diversity. After formalizing the gaps and needs, the second step will be for
484   international organizations like IPBES (http://www.ipbes.net/) to urge the development of better
485   biodiversity monitoring programs. New initiatives like GEO BON (Scholes et al.
486   2008, http://geobon.org/) are taking the first important steps towards establishing a group of
487   biodiversity observation networks around the globe, but the funding needed to organize and
488   sustain efforts in poor and developing countries is chronically lacking. Technological
489   innovations may complement research networks by allowing individual experts or citizen
490   scientists to track and monitor biodiversity from any given location using their cell phones (e.g.,
491   Goldsmith 2015). Ultimately, these efforts may produce a lot of data with high taxonomic
492   resolution for some species groups, but it will likely have limits in spatial, temporal and
493   taxonomic resolution and scale. Therefore, new technologies that can monitor additional aspects
494   of biodiversity with high spatial and temporal resolution will be important tools for truly

495 representative monitoring of biodiversity (Asner et al. 2015, Pimm et al. 2015). If we progress to
496 a set of monitoring programs with good spatial, temporal, and taxonomic resolution, and
497 coordinated data collection, then we will be in a position to improve analyses of local
498 biodiversity change (e.g. Azaele et al. 2015).

499 *A Challenge* - Lastly, the Vellend et al. (2013) and Dornelas et al. (2014) data syntheses point to
500 a challenge we must meet if we are to accurately quantify diversity change on the planet. Many
501 landscapes are mosaics of habitats that have been subjected to both direct and indirect human
502 influences. Farm fields or urban areas have experienced direct human influence where much
503 plant and animal life have been destroyed and replaced with lower diversity land cover. While
504 such areas can harbor populations of functionally important species (Wolters et al. 2000), the
505 direct effects that people have on local biodiversity through habitat destruction or conversion are
506 typically negative. In contrast, adjacent habitat fragments have not been destroyed, and represent
507 areas where humans may increase species richness (e.g., species introductions) or decrease
508 richness (e.g., fragmentation, pollution; see Haddad et al. 2015) and alter community
509 composition (Wardle et al. 2011). Future efforts to quantify changes in local biodiversity must
510 simultaneously account for the direct effects that people have on biodiversity through habitat
511 destruction, or conversion, and the indirect effects (both positive and negative) humans have on
512 remaining or recovering habitats. Only by simultaneously considering both the direct and
513 indirect causes of biodiversity change on a landscape will we be able to provide accurate
514 estimates of local biodiversity change.

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695

696   SUPPORTING INFORMATION

697   Appendix S1: Detailed methods and additional results are given for the analyses on the spatial

698   representation of the datasets and the findings of the simulations analyzing time series duration.FIGURE

699   LEGENDS

700   Figure 1. Spatial bias of the Vellend et al. (2013) and Dornelas et al. (2014) data syntheses. On

701   the left are the maps (with sources) used to represent the global distributions of terrestrial

702   vascular plant richness, human impacts on forest cover (pixels classified as loss, gain or loss and

703   gain in forest cover by Hansen et al. 2014; see Fig. S1 for other human impacts on terrestrial

704   ecosystems) marine species richness, and human impacts on the oceans. On the x-axis

705   Hellinger's distance $d$ quantifies the amount of spatial basis in any collection of sampling sites

706   relative to the global map. The box plots in the middle of the figure show the distribution of $d$-

707   values for 1000 random collections of samples where the number of samples in that collection

708     equals the number of study sites used in the Vellend et al. (terrestrial) or Dornelas et al. (marine)

709     syntheses. Any randomly sampled, spatially representative sample of Earth's diversity, or of

710     human impacts on Earth's ecosystems, should fall within the expected distributions given by the

711     box plots. Hellinger distances showing actual spatial bias of terrestrial systems for studies

712     collated by Vellend et al. and Dornelas et al. are shown with green and blue stars, respectively.

713     Figure 2. Sources of spatial bias in the Vellend et al. (A-C) and Dornelas et al. (D-E) data

714     syntheses. Panels A and D show kernel density maps illustrating the primary clusters of study

715     locations used in the Vellend et al. terrestrial (A), and Dornelas et al. marine (D) syntheses. The

716     y-axis in panels B, C, E, and F all show the log ratio representing the number of observed sites

717     included in the synthesis relative to the number of sites that would be expected to occur in a

718     random sample from an area that is proportional to the area of (B) different Olsen biomes on the

719     land surface of the planet, (C) categories of land-use change in the Hansen Forest Cover Change

720     map, (E) the world's major oceanic systems, and (F) categories representing increasing numbers

721     of anthropogenic stressors from the Halpern et al. (2008) map of human impacts on oceans. Any

722     log ratio $y > 0$ indicates that the category on the x-axis is represented $e^y$ more in the data

723     synthesis than it should be based on a random and proportional sampling effort. Any log ratio y

724     $< 0$ indicates that the category on the x-axis is represented $e^{-y}$ less than it should be based on a

725     random, proportional sampling effort. 1 = Tropical & Subtropical Moist Broadleaf Forests, 2 =

726     Tropical & Subtropical Dry Broadleaf Forests, 4 = Temperate Broadleaf & Mixed Forests, 5 =

727     Temperate Coniferous Forests, 6 = Boreal Forests, 7 = Tropical & Subtropical Grasslands &

728     Savannas & Shrublands, 8 = Temperate Grasslands & Savannas & Shrublands, 9 = Flooded

729     Grasslands & Savannas, 10 = Montane Grasslands & Shrublands, 11 = Tundra, 12 =

730     Mediterranean Forests & Woodlands & Scrub, 13 = Deserts & Xeric Shrublands.

731     Figure 3. Plotting effect size $\ln(SR_{t2}/SR_{t1})$ as a function of duration reveals a significant negative

732     relationship for a) Vellend et al. (2013) and b) Dornelas et al. (2014) datasets. See main text for

733     statistical effects of duration.

734     Figure 4. Effects of reference state on estimates of species loss. A) Two hypothetical time series

735     of species richness for a disturbed and reference (undisturbed) site. B) Comparison of disturbed

736     with reference site using LRR, $\ln(SR_{disturbed}/SR_{reference})$ at each time point in the series. The LRR

737     is consistently negative because the disturbed site always maintains fewer species than the

738     reference site. C) Comparison of the final point at the disturbed site with all previous time points

739   at the disturbed site using LRR, $\ln(SR_{final}/SR_{t0})$, for t-1, t-2, … t-25. The series of LRR values is

740   positive for most of the comparisons with the past, capturing recovery of species richness.

741   Figure 5. Re-analysis of the data from Vellend et al. The original dataset included two types of

742   studies - those showing how local richness is affected by some driver (impact) and those focused

743   on how richness recovers following effects of a driver (recovery). We re-analyzed effect sizes in

744   the Vellend et al. dataset (the LRR of mean richness in final vs. initial surveys) using a mixed

745   model ANOVA with 'STUDY' included as a random effect and observations weighted by square

746   root of sample size (as the authors did). The effect sizes are calculated using both types of studies
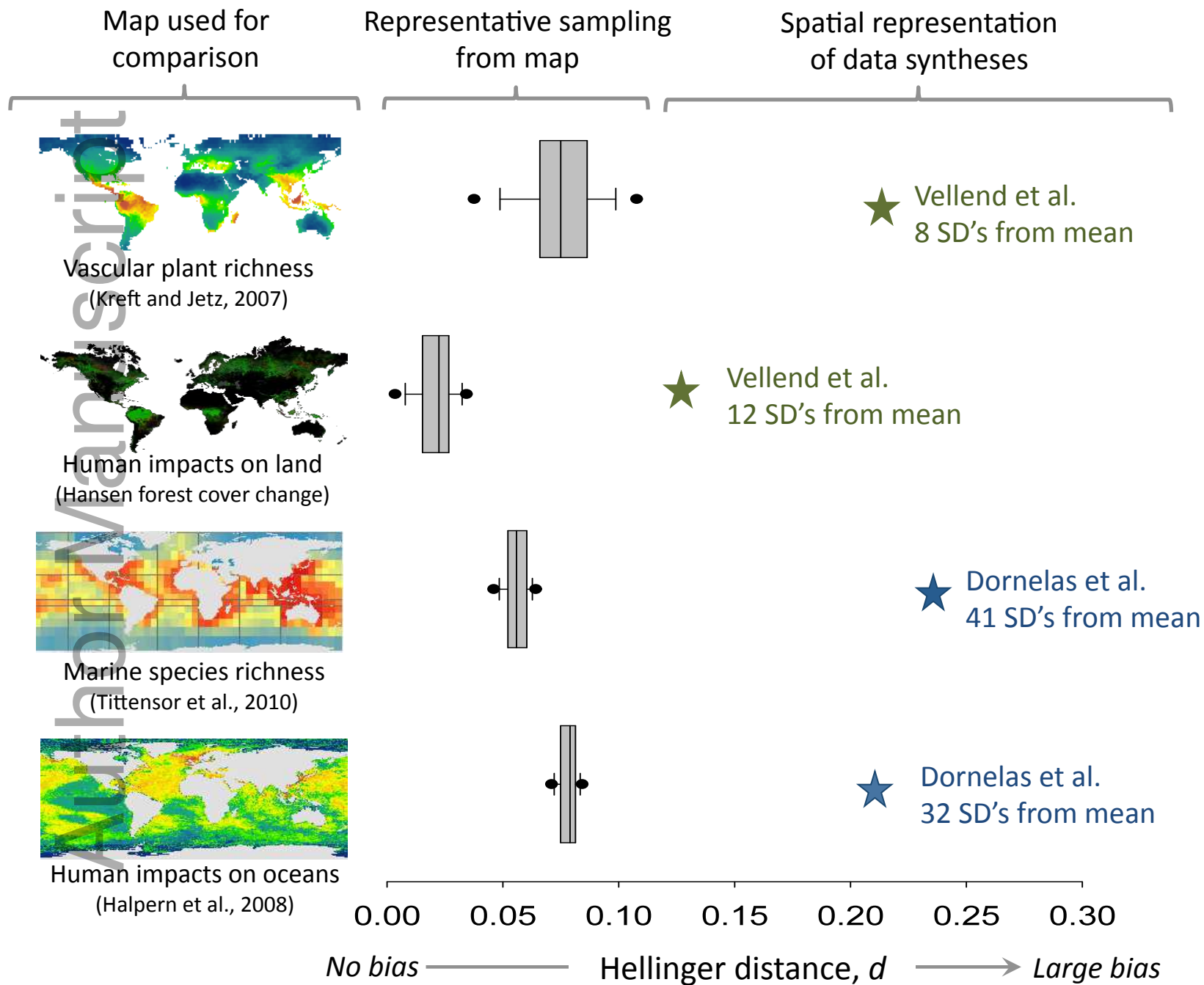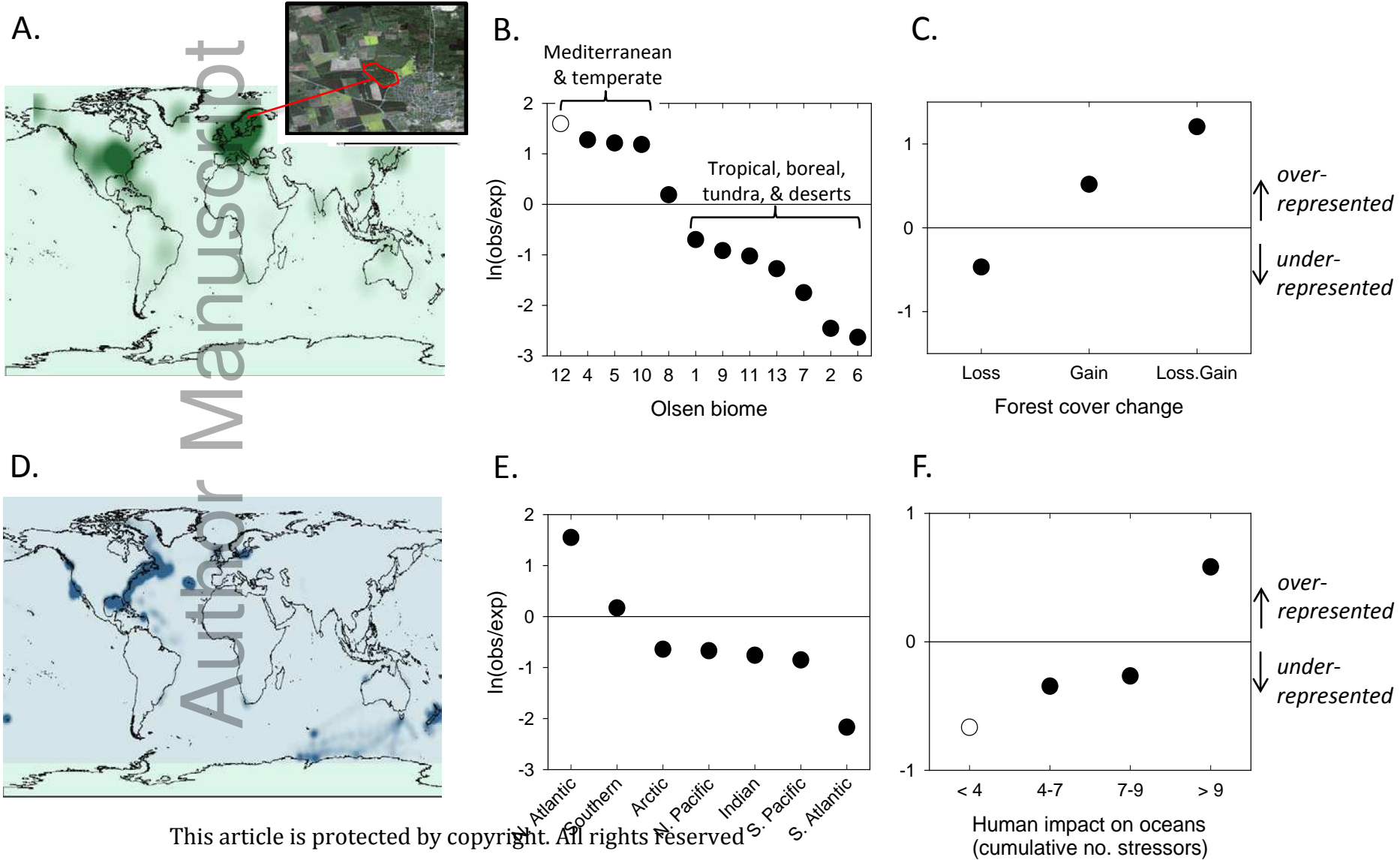
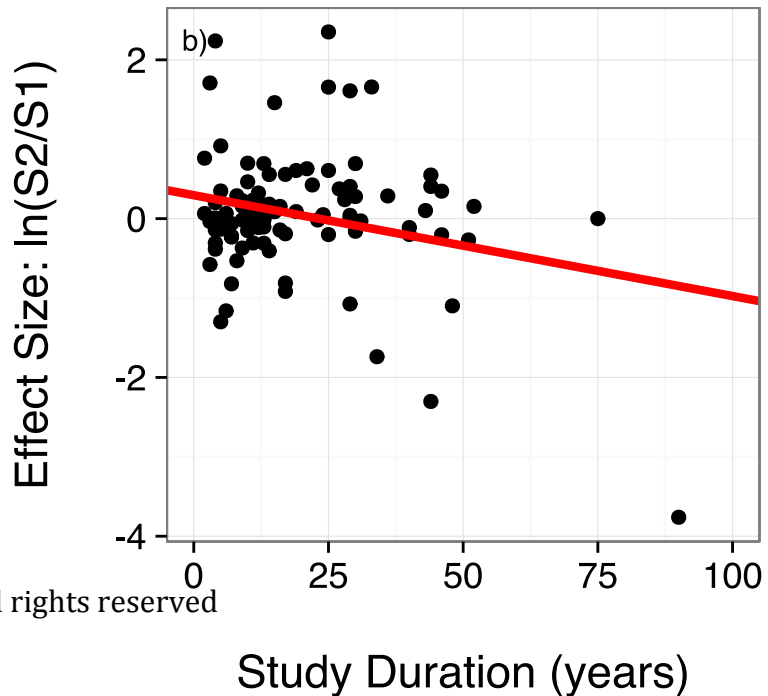747   and with studies assessing direct impact only.

Map used for comparison

Representative sampling from map

Spatial representation of data syntheses

Vascular plant richness
(Kreft and Jetz, 2007)

Human impacts on land
(Hansen forest cover change)

Marine species richness
(Tittensor et al., 2010)

Human impacts on oceans
(Halpern et al., 2008)

Vellend et al.
8 SD's from mean

Vellend et al.
12 SD's from mean

Dornelas et al.
41 SD's from mean

Dornelas et al.
32 SD's from mean

0.00   0.05   0.10   0.15   0.20   0.25   0.30

*No bias* ⟶ Hellinger distance, $d$ ⟶ *Large bias*

Figure 2

ecy_1427_f2.pptx

# Vellend et al.
ecy_1427_f3.pdf

# Dornelas et al.



a)

Effect Size: ln(S2/S1)

Study Duration (years)

b)

Effect Size: ln(S2/S1)
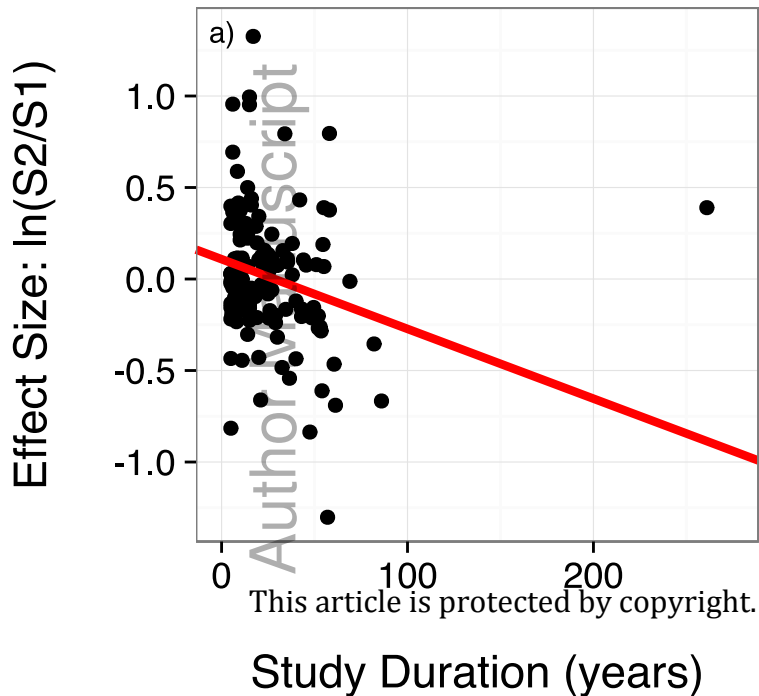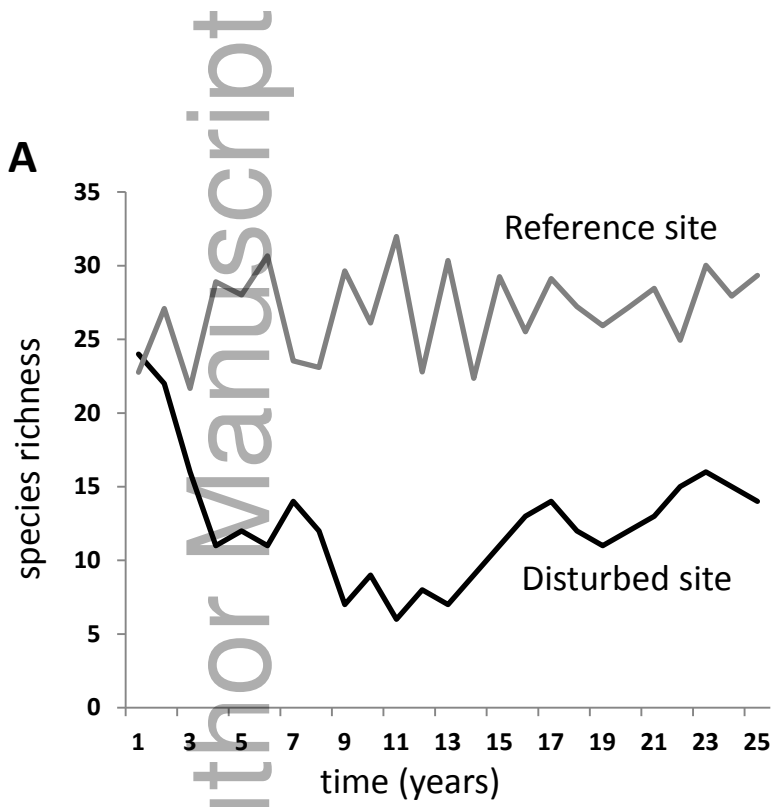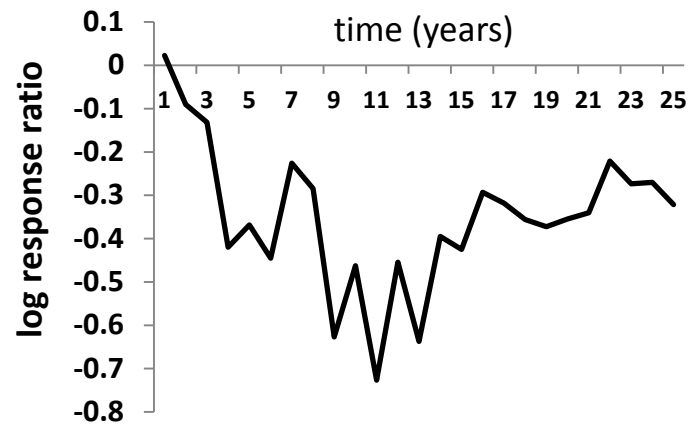
Study Duration (years)

Figure 4

ecy_1427_f4-5.pptx



**B** Comparison with reference site through time

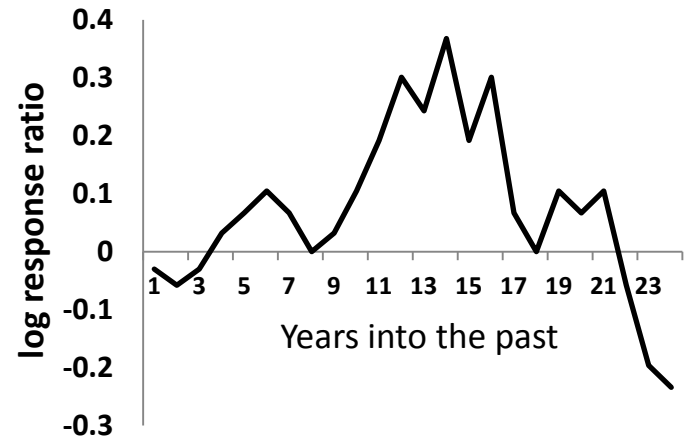**C** Final time point of the time series compared to earlier time points from the disturbed site only

Figure 5

(B)