

Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity

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Abstract. Global species extinction rates are orders of magnitude above the background rate documented in the fossil record. However, recent data syntheses have found mixed evidence for patterns of net species loss at local spatial scales. For example, two recent data meta-analyses have found that species richness is decreasing in some locations and is increasing in others. When these trends are combined, these papers argued there has been no net change in species richness, and suggested this pattern is globally representative of biodiversity change at local scales. Here we reanalyze results of these data syntheses and outline why this conclusion is unfounded. First, we show the datasets collated for these syntheses are spatially biased and not representative of the spatial distribution of species richness or the distribution of many primary drivers of biodiversity change. This casts doubt that their results are representative of global patterns. Second, we argue that detecting the trend in local species richness is very difficult with short time series and can lead to biased estimates of change. Reanalyses of the data detected a signal of study duration on biodiversity change, indicating net biodiversity loss is most apparent in studies of longer duration. Third, estimates of species richness change can be biased if species gains during post-disturbance recovery are included without also including species losses that occurred during the disturbance. Net species gains or losses should be assessed with respect to common baselines or reference communities. Ultimately, we need a globally coordinated effort to monitor biodiversity so that we can estimate and attribute human impacts as causes of biodiversity change. A combination of technologies will be needed to produce regularly updated global datasets of local biodiversity change to guide future policy. At this time the conclusion that there is no net change in local species richness is not the consensus state of knowledge.

Key words: Anthropocene; baselines; biodiversity monitoring; extinction; invasion; meta-analysis; species richness; time series.

INTRODUCTION

Humans are affecting the abundance and distribution of species across the planet, and these impacts are projected to increase in the 21st century (Pereira et al. 2010, Pimm et al. 2014). As much as 50% of the Earth's ice-free land surface has been transformed into agriculture and urban land cover (Ellis and Ramankutty 2008), one-third of all forest has been cleared and most of the rest is fragmented (Haddad et al. 2015), the ocean is heavily impacted (Halpern et al. 2008), and virtually all land has been affected by pollution and climate

change. Since 1600, an estimated 906 known species have gone extinct globally (IUCN 2015). While this represents a small fraction of the world's eight or more million species of eukaryotes (Mora et al. 2011), the rate of extinction (>900 species in ca. 400 yr) is 100–1,000 times the historical rate in the fossil record (Pimm et al. 2014, Ceballos et al. 2015). Moreover, more than 20,000 species are now threatened with extinction—a number that has doubled since 2000 (IUCN 2015). Uncertainty exists about the rate of global extinction due to incomplete sampling and identification of most of the remaining biodiversity on Earth (Regnier et al. 2015), the time lag between human impacts and extinction (Gilbert and Levine 2013, Essl et al. 2015a), and the extent to which extinctions might be offset by speciation (Thomas 2013). Even so, consensus has

Manuscript received 29 September 2015; revised 8 February 2016; accepted 11 February 2016; final version received 10 March 2016.
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emerged that Earth is in the midst of an exceptional global extinction event that is unprecedented in the history of human life (Periera et al. 2010, Pimm et al. 2014, Ceballos et al. 2015, Regnier et al. 2015).

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

Alongside evidence of local biodiversity loss, however, a number of papers have shown that human impacts can also increase diversity at sub-global scales (Stohlgren et al. 1999, Sax et al. 2002, McKinney 2008, Ellis et al. 2012, Elahi et al. 2015). The success of some species in human-dominated landscapes (Aronson et al. 2014), increases in local diversity due to disturbance (DeVictor and Robert 2009), and the spread of exotic species (e.g., Bruno et al. 2004) are all examples. When these additions match or outpace the rate of local species extinctions, then diversity in any particular location can stay the same (Byrnes et al. 2007), increase (Sax et al. 2002, Elahi et al. 2015), or show high rates of species turnover (Dornelas et al. 2014).

While there is growing recognition that human activities may either increase or decrease local biodiversity, the data have generally been insufficient to quantify long-term trends in biodiversity change at local scales throughout the world, and to reconcile them with global estimates of species loss. To address this data gap, several recent studies have collated datasets that provide direct estimates of biodiversity change through time at local scales (e.g., Vellend et al. 2013, Dornelas et al. 2014, Hudson et al. 2014, Elahi et al. 2015, Newbold et al. 2015). Among these, two data syntheses have

reached the conclusion that there is no evidence for systematic declines in species richness at local scales and claimed that their conclusions are globally representative of what is happening to species richness at local spatial scales (Vellend et al. 2013, Dornelas et al. 2014). Here we challenge the conclusions of these two syntheses on three grounds: (1) we present new analyses showing the datasets assembled for these syntheses exhibit extreme spatial bias, and are not globally representative of species richness or human impacts on ecosystems that influence biodiversity; (2) we reanalyze these data and detect a signal of study duration on biodiversity change, indicating net biodiversity loss is most apparent in studies of longer duration. Ancillary simulations show that trends estimated with short time series can be biased; (3) we show why a lack of appropriate historical baselines or spatial references precludes these studies from accurately characterizing species richness change due to humans. After laying out our critique, we reflect on some lessons learned from these syntheses, and describe new challenges in accurately quantifying changes in biodiversity on this planet.

THREE ESSENTIAL CONSIDERATIONS IN ASSESSMENTS OF LOCAL BIODIVERSITY CHANGE

The synthesis completed by Vellend et al. (2013) focused on patterns of biodiversity change in terrestrial vascular plants, and claimed to be “a systematic global meta-analysis of plant species diversity change over time in $>16,000$ plots from all major vegetation types, including areas under profound and direct human influence.” Data used for this synthesis came from 346 existing studies that had monitored $>16,000$ nonexperimental, “local-scale” vegetation plots for anywhere between 5 and 261 yr. Vellend et al. (2013) summarized these time-series by calculating log response ratios (LRR) that quantified the proportional change in plant species richness from the initial to final year of the study, and divided LRR by the number of decades to arrive at a proportional rate of species loss. The synthesis completed by Dornelas et al. (2014) collated data from scientific papers and publicly available databases that: (1) had time-series of >3 yr, (2) used consistent sampling methodology, and (3) reported abundance estimates for all species in samples. Their final dataset comprised 100 time-series representing 35,613 species of mammals, birds, fishes, invertebrates, and plants measured at sites and along marine transects including 430,324 latitude and longitude coordinates. Although the synthesis claimed to cover marine, freshwater, and terrestrial systems, the vast majority of data points included in Dornelas et al. (2014) were from marine systems, primarily from cruises that had monitored plankton, or from seabird, fish, and cetacean monitoring programs. In this section, we raise three criticisms of these two data syntheses that call into questions their primary conclusions about local change in species richness.

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

The datasets collated by Vellend et al. (2013) and Dornelas et al. (2014) included a large number of observations taken from many locations around the globe over multiple decades. However, as is true for most syntheses of existing data, they represented an opportunistic collection of studies that were designed for a wide variety of purposes. The choice of which studies to include in these syntheses was not guided by a geographically explicit sampling design. The authors assembled any and all time-series they could find that matched their search criteria in which someone, somewhere, had repeated measures of

species richness at the same site for any purpose. The key question in this case is whether the data collated for these syntheses are sufficiently representative of the global distribution of species richness or human impacts on ecosystems such that they are broadly representative of what is happening locally to species richness around the globe.

To assess how well the Vellend et al. (2013) and Dornelas et al. (2014) syntheses capture a globally representative sample of species richness and human impacts on ecosystems, we quantified spatial bias in these datasets. We began by locating existing maps of species richness and human impacts on ecosystems that represent the most spatially resolved information available at a global scale (see Fig. 1 and Appendix S1: Table S1). For marine biodiversity, we used the United Nations Environmental

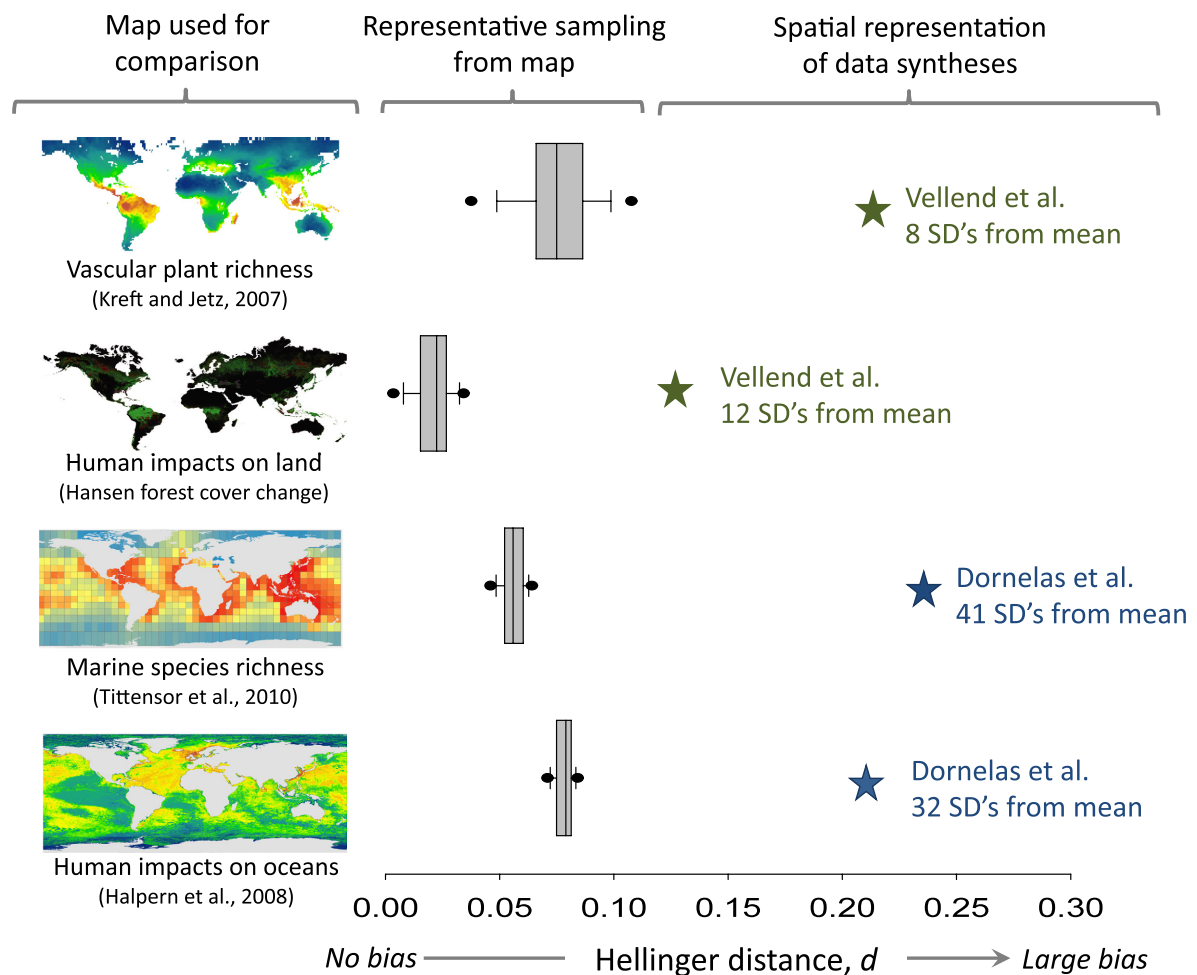


FIG. 1. Spatial bias of the Vellend et al. (2013) and Dornelas et al. (2014) data syntheses. On the left are the maps (with sources) used to represent the global distributions of terrestrial vascular plant richness, human impacts on forest cover (pixels classified as loss, gain, or loss and gain in forest cover by Hansen et al. 2013, see Appendix S1: Fig. S1 for other human impacts on terrestrial ecosystems) marine species richness, and human impacts on the oceans. On the x -axis Hellinger's distance d quantifies the amount of spatial bias in any collection of sampling sites relative to the global map. The box plots in the middle of the figure show the distribution of d -values for 1,000 random collections of samples where the number of samples in that collection equals the number of study sites used in the Vellend et al. (terrestrial) or Dornelas et al. (marine) syntheses. Any randomly sampled, spatially representative sample of Earth's diversity, or of human impacts on Earth's ecosystems, should fall within the expected distributions given by the box plots. Hellinger distances showing actual spatial bias of terrestrial systems for studies collated by Vellend et al. and Dornelas et al. are shown with green and blue stars, respectively.

Programme World Conservation Monitoring Centre's map of global marine biodiversity (Tittensor et al. 2010). For terrestrial plant biodiversity, we used the global map of vascular plant species richness published by Krefl and Jetz (2007, their Fig. 3d). For human impacts on the oceans, we used the Halpern et al. (2008) global map of human impacts on marine ecosystems, which tallies the number of anthropogenic stressors being imposed on oceans as a metric of cumulative impact. For human impacts on land, we used the Hansen Forest Cover Change dataset, which has utilized Landsat images since 2000 to quantify the extent and conversion of forested habitats globally (Hansen et al. 2013). In addition to forest cover change, we compared the Vellend et al. (2013) dataset to the HYDE 3.1 database (Goldewijk et al. 2010) that quantifies conversion of Earth's land surface to agricultural or pastoral habitat, and a map of the Human Global Influence Index (Goldewijk et al. 2010) that quantifies human built infrastructure like cities and roads. It is important to be clear that none of these maps of human impact on the world's terrestrial or marine environments were specifically designed to quantify impacts on biodiversity per se. As such, conclusions drawn from these maps are only as good as the assumption that they accurately portray human impacts on biodiversity. Nevertheless, we use these maps because they are presently some of the most comprehensive, and spatially resolved approximations of human stressors being imposed on the world's ecosystems.

For each of the terrestrial and marine maps used in our analysis (see Fig. 1), we randomly sampled N locations across the globe, where N was equal to the number of sites that were collated for use in the Vellend et al. (2013) synthesis (or 10,000 points for the Dornelas et al. (2014) synthesis: see Supplemental Material for justification). For each random sample of N locations, we quantified the amount of spatial bias in those locations using Hellinger's distance d (Schmuller et al. 2014, supplemental material). As N becomes increasingly large and approaches the sampling of every location L (a pixel on a map), there is no spatial bias in a sample and d becomes zero because the map has been exhaustively sampled. However, because N is always less than L , even a random sampling of N points will have some spatial bias associated with that sample. By performing this random sampling effort 1,000 times for each map, we generated expected distributions that represent the amount of spatial bias one would expect to occur for a sample composed of N studies, but where those studies were chosen in an unbiased manner, with regard to species richness or human impact across space (further details of the analyses are given in Supplemental Material). Any random, spatially representative sample of Earth's diversity, or of human impacts on Earth's ecosystems, should fall within these expected distributions (Fig. 1).

The studies collated for both the Vellend et al. (2013) and Dornelas et al. (2014) syntheses fell well outside the distributions generated from representative sampling,

with values of Hellinger's d that were indicative of extreme spatial biases (Fig. 1). The collection of studies collated by Vellend et al. (2013) was eight standard deviations outside the mean of a spatially representative sample of terrestrial vascular plant richness, and 12 standard deviations from the mean of a representative sample of forest cover change. Comparison of the Vellend et al. (2013) dataset to global maps of land converted to cropland/pasture habitat, or converted to human infrastructure similarly revealed biases ranging from 18 to 27 standard deviations from a representative sample (see Appendix S1: Fig. S1). The causes of these spatial biases are obvious from looking at a kernel density map showing the geographic concentration of studies included in the Vellend et al. (2013) synthesis (Fig. 2A). The vast majority of studies included in the Vellend et al. (2013) synthesis were performed in the United States and the European Union—a set of developed countries that have historically had stronger than average financial support for biological and environmental science programs. Given the predominance of data from these two regions of the globe, temperate forests, temperate grasslands, and Mediterranean forests and woodlands were over-represented by as much as $e^{1.60} = 5$ times their proportional area of Earth's terrestrial land surface relative to all other terrestrial vegetated habitats (Fig. 2B). In contrast, tropical biomes that harbor the greatest terrestrial biodiversity, but where monitoring programs are rare, were under-represented by as much as $e^{-2.46} = 0.09$ times their proportional area of Earth's terrestrial land surface (Fig. 2B). Boreal forests, deserts, and tundra were also under-represented.

Studies collated for the Vellend et al. (2013) synthesis also under-represented areas of the planet that have been most heavily impacted by humans through forest clear-cutting (Fig. 2C). The 'loss' category from the Hansen forest cover change map was under-represented by $e^{-0.47} = 0.6$ times of the areal representation on Earth, of which, 32% occurs in the tropics where Vellend et al. (2013) had little data. In contrast, the Vellend et al. (2013) synthesis over-represented areas where forests are now recovering after logging or natural disaster by $e^{0.52} = 1.7$ times the areal coverage of these habitats (Fig. 2C, gain), and over-represented the loss-and-gain category that generally describes areas of high-intensity, short-cycle forestry (Hansen et al. 2013). This latter category (loss + gain), which is common in the southeastern United States, represents only 0.14% of the total land area on the planet; yet the number of pixels in this category within the Vellend et al. (2013) dataset was 3.7 times greater than a representative sample.

The potential implications of these spatial biases for estimating changes in biodiversity are made more obvious by taking a closer look at a particular case study. The inset in Fig. 2A shows the location of Dalby Söderskog National Park in Sweden, which represents a 0.36 km² forest fragment in a landscape where nearly all of the historical forest has been converted to agricultural

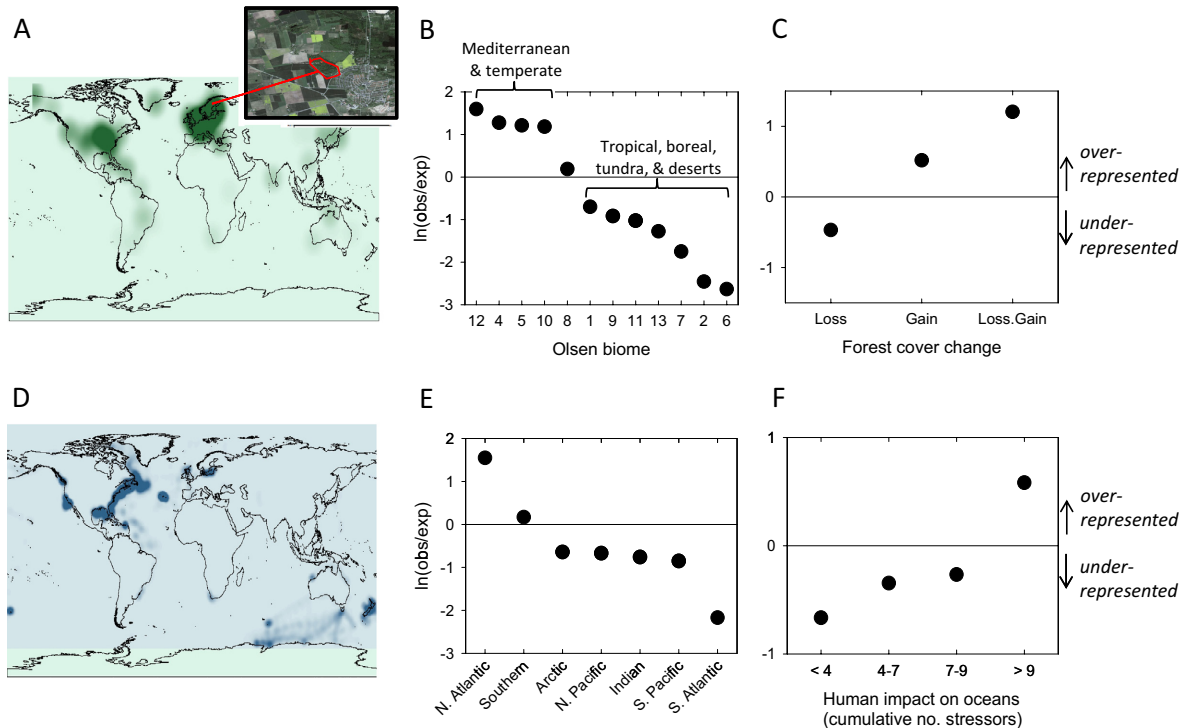


FIG. 2. Sources of spatial bias in the Vellend et al. (A–C) and Dornelas et al. (D–F) data syntheses. Panels A and D show kernel density maps illustrating the primary clusters of study locations used in the Vellend et al. terrestrial (A), and Dornelas et al. marine (D) syntheses. The y -axis in panels B, C, E, and F all show the log ratio representing the number of observed sites included in the synthesis relative to the number of sites that would be expected to occur in a random sample from an area that is proportional to the area of (B) different Olsen biomes on the land surface of the planet, (C) categories of land-use change in the Hansen Forest Cover Change map, (E) the world's major oceanic systems, and (F) categories representing increasing numbers of anthropogenic stressors from the Halpern et al. (2008) map of human impacts on oceans. Any log ratio $y > 0$ indicates that the category on the x -axis is represented e^y more in the data synthesis than it should be based on a random and proportional sampling effort. Any log ratio $y < 0$ indicates that the category on the x -axis is represented e^{-y} less than it should be based on a random, proportional sampling effort. 1 = Tropical & Subtropical Moist Broadleaf Forests, 2 = Tropical & Subtropical Dry Broadleaf Forests, 4 = Temperate Broadleaf & Mixed Forests, 5 = Temperate Coniferous Forests, 6 = Boreal Forests, 7 = Tropical & Subtropical Grasslands & Savannas & Shrublands, 8 = Temperate Grasslands & Savannas & Shrublands, 9 = Flooded Grasslands & Savannas, 10 = Montane Grasslands & Shrublands, 11 = Tundra, 12 = Mediterranean Forests & Woodlands & Scrub, 13 = Deserts & Xeric Shrublands.

or urban cover. The time-series included in the Vellend et al. synthesis was from a study that had documented a loss of ~ 3 species in this forest fragment over a period of 69 yr. Vellend et al. (2013) explicitly excluded from their study any sites with direct land-use conversion such as clear-cutting and conversion to urban and agricultural habitat, arguing that in such cases “any effect of a change in the number of species on ecosystem function will be negligible compared with the effects of other changes... [on ecosystem function]” (Vellend et al. 2013). However, failure to consider diversity change in the majority of a landscape where most of the habitat has been destroyed invalidates one of the main conclusions of this synthesis: that plant biodiversity is not generally declining at local spatial scales.

The data collated for the Dornelas et al. (2014) synthesis were even more spatially biased, lying 41 standard deviations outside the mean of a spatially representative sample of marine species richness, and 32 standard deviations from the mean of a representative sample of human

impacts on the world's oceans. Although the Dornelas et al. (2014) synthesis was based on samples taken at $>430,000$ latitude-longitude coordinates, a kernel density map of geographic locations shows that the vast majority of sampling sites stemmed from cruises in the Northern Atlantic ocean along the coasts of the United States and Europe and, to a lesser extent, from cruises departing from Australia to study the Antarctic shelf (Fig. 2D). As a result, the North Atlantic was over-represented in the dataset by $e^{-1.55} = 4.7$ times (Fig. 2E). In contrast, there was little representation of data from the North or South Pacific, the Indian Ocean, or the Arctic Ocean, all of which were represented by 50% less than they should have been given their proportional surface area of the planet. Thus, the Dornelas et al. (2014) dataset was only representative of one of the world's major oceans, and had almost no data from those areas that rank among the most diverse marine habitats on Earth (e.g., the Indo-Pacific and Indian oceans). The Dornelas et al. (2014) dataset did, however, over-represent marine habitats

where Halpern et al. (2008) suggest the cumulative number of anthropogenic stressors is the highest. This representation is perhaps not unexpected given the preponderance of sampling sites along the coastal U.S. and Europe where human impacts on marine ecosystems are most well documented. The lack of a decline in richness despite heavy representation from impacted areas is interesting and unexpected. Potential reasons for local increases include species invasions, recovery from historical overfishing, indirect effects of overfishing on lower trophic levels, or climate warming. Thus a more in depth investigation of these individual drivers, rather than just a cumulative impact score, is warranted.

Our analyses show that the datasets collated and analyzed by Vellend et al. (2013) and Dornelas et al. (2014) are not spatially representative of species diversity or human impacts on land or in the oceans. The extreme spatial bias of these datasets means that the inferences Vellend et al. (2013) and Dornelas et al. (2014) made from their data to the rest of the globe are unfounded (Environmental Protection Agency 2002). Their conclusions are limited to a select subset of well-studied locations on the planet, namely the U.S., Europe and, to a lesser extent, the Antarctic shelf. Furthermore, for both data syntheses, the authors assembled data that under represent areas of the planet that are undergoing major land use transitions (e.g., current deforestation, conversion to agricultural or urban habitats, loss of coral reefs). Finally, for the Vellend et al. (2013) synthesis, terrestrial habitats that are in recovery from past deforestation or managed for timber harvest followed by succession are highly over-represented. This suggests their conclusions may be more representative of the accrual of species in successional or recovering ecosystems, than the loss of species resulting from human impacts on the original system.

Estimates of biodiversity change are systematically biased when syntheses are based on datasets composed primarily of short time series

Vellend et al. (2013) and Dornelas et al. (2014) found no average trend in local biodiversity when time series were pooled from many geographical regions, ecosystem types and taxonomic groups. However, short time series have low power to detect a trend and can produce biased estimates of the trend itself if the time series are nonlinear and nonstationary (Bence 1995, Peters and Mengerson 2008, Mengersen et al. 2013). In Supporting Information, we show through simulation that LRR (used by Vellend et al. 2013) and regression (used by Dornelas et al. 2014) on short time series inadequately estimate a known trend of declining richness (Appendix S1: Figs. S2 and S3). Crucially, we show that meta-analytic datasets dominated by short time-series have potential to bias conclusions, and longer duration time series provide the most reliable estimates of the known underlying temporal trend in biodiversity. These results lead us to reanalyze

the data of both Vellend et al. and Dornelas et al. to look at how their conclusions may have been influenced by the duration of the studies they collated.

Re-analysis of the effect of duration

Vellend et al. (2013) and Dornelas et al. (2014) considered the importance of study duration in their analyses, but both concluded that study duration had no effect on mean local biodiversity change, even though the datasets contained few time series greater than 50 years. Vellend et al. (2013) calculated a rate of biodiversity change by dividing the effect size by duration ($\text{Effect Size} = \ln(\text{SR}_{t2}/\text{SR}_{t1})/\text{duration}$). Including duration in the denominator, rather than as a covariate of the log ratio can reduce the power to detect an effect. To reevaluate the possibility that longer duration time series are more likely to reveal trends in species diversity, we reanalyzed data in Vellend et al. (2013) and Dornelas et al. (2014) with linear mixed models using study duration as a predictor of local biodiversity change. Biodiversity change was measured as the log ratio of species richness at the end vs. beginning of each data set ($\text{Effect Size} = \ln[\text{SR}_{t2}/\text{SR}_{t1}]$), consistent with Vellend et al. (2013) because only first and last estimates are available. We used duration (number of years of the study) so that our estimates of the duration coefficient would be directly comparable to the results of the models in Vellend et al. (2013) and Dornelas et al. (2014). Evaluation of residuals and leverage suggested no need to log transform duration. For the Vellend et al. data a linear mixed model with a random effect of duration (slope) and intercept revealed a negative relation between biodiversity change and time series duration (Fig. 3A; slope = -0.004 se = 0.002 , $P = 0.04$) with 4% species loss observed after 10 yr, and an average 17% loss after 50 yr. Analysis of the Dornelas et al. (2014) data using log ratios (rather than fitting a linear regression, as done originally) reveals a stronger negative relationship between biodiversity change and study duration (Fig. 3B; slope = -0.01 se = 0.005 , $P = 0.01$, reflecting, on average, a decline of 10% after 10 yr and 40% loss after 50 yr. In our reanalysis, this relationship is sensitive to the inclusion of its longest datasets, potentially reflecting a drawback of using the log-ratio approach to detect change. The net effect of incorporating study duration into an analysis of richness change in these data sets suggests that species richness may, on average, be declining, with 4–10% loss after 10 yr and 18–40% loss after 50 yr.

Why should longer time series suggest systematic diversity loss while shorter studies do not? In addition to the statistical issues outlined above, one potential biological reason that species loss may only be detected in multi-decade time-series is that local extinctions can be delayed and occur very slowly especially in remnant ecosystems experiencing the legacies of direct and indirect human impacts (Essl et al. 2015b, Haddad et al. 2015). Because of extinction lags, short duration surveys are unlikely to reveal a signal of loss against a background of

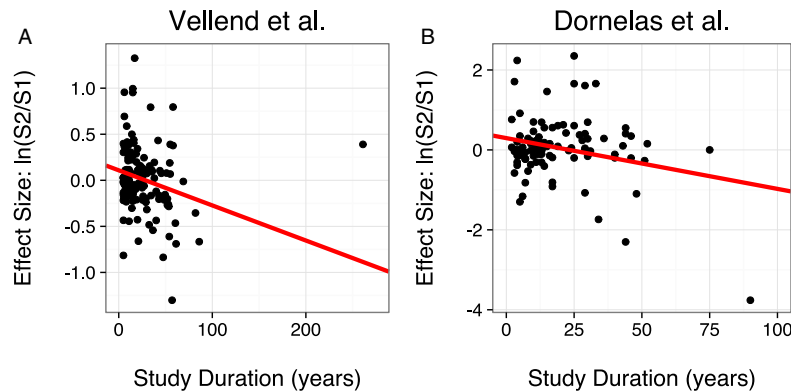


FIG. 3. Plotting effect size $\ln(SR_2/SR_1)$ as a function of duration reveals a significant negative relationship for (A) Vellend et al. (2013) and (B) Dornelas et al. (2014) datasets. See main text for statistical effects of duration.

local colonization and extinction events, if the survey occurred before the extinction debts have been realized. In fact, empirical analyses of extinction debts have shown that they may take more than a century to detect (e.g., Dullinger et al. 2013, Gilbert and Levine 2013, Essl et al. 2015b). We suggest, therefore, that study duration should be an important feature of study design for the estimation of local biodiversity loss in future meta-analyses. More data, especially longer time series, are required to reveal trends that are hidden because they occur slowly or because there is a time lag years after their causes (Magnuson 1990).

Estimates of biodiversity change can be biased if species gains during post-disturbance recovery are included without also including species losses that occurred during the disturbance. Net species change should be assessed with respect to a historical baseline or spatial reference communities

Recent meta-analyses have inconsistent results partly because changes in biodiversity have been defined and measured against different baselines. In earlier studies finding that anthropogenic disturbances tend to decrease local biodiversity (Benayas et al. 2009, Jones and Schmitz 2009, Murphy and Romanuk 2013), changes in biodiversity were measured against a common baseline: levels of local biodiversity observed in intact ecosystems, with minimal human disturbance. In contrast, recent meta-analyses of time series (Vellend et al. 2013, Dornelas et al. 2014, Elahi et al. 2015) have measured changes in biodiversity against levels of local biodiversity observed at earlier points in time, when ecosystems might have been more or less disturbed by people than during recent observations. These two approaches will yield not only quantitatively different results, but also qualitatively different results; net species losses measured against a mostly undisturbed baseline can appear as species gains when measured against a highly disturbed baseline. Consider the case where a disturbance causes biodiversity loss, and then relaxation of this disturbance results in recovery of

biodiversity, as observed in hundreds of previous studies (Fig. 4; Benayas et al. 2009, Jones and Schmitz 2009). The former approach, which uses remnant ecosystems as a spatial reference site (Fig 4B), would only conclude the recovery to result in net species gains if there are more species gains during recovery than there were species losses during the disturbance. In contrast, the latter approach (Fig 4C) would see all species gains that occurred during recovery as net species gains if the time series started after the disturbance occurred.

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

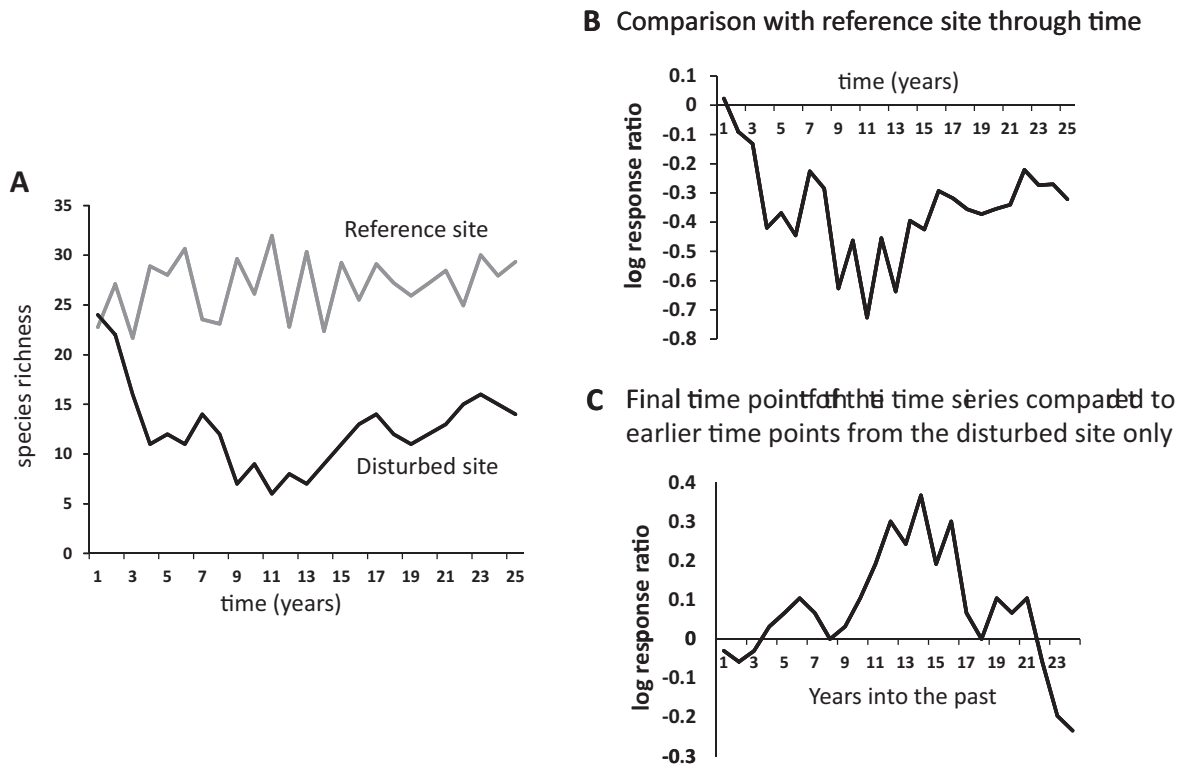


FIG. 4. Effects of reference state on estimates of species loss. (A) Two hypothetical time series of species richness for a disturbed and reference (undisturbed) site. (B) Comparison of disturbed with reference site using LRR, $\ln(SR_{\text{disturbed}}/SR_{\text{reference}})$ at each time point in the series. The LRR is consistently negative because the disturbed site always maintains fewer species than the reference site. (C) Comparison of the final point at the disturbed site with all previous time points at the disturbed site using LRR, $\ln(SR_{\text{final}}/SR_{t_0})$, for $t-1, t-2, \dots, t-25$. The series of LRR values is positive for most of the comparisons with the past, capturing recovery of species richness.

Dornelas et al. (2014) did not provide information on which marine time series were taken from sites where biodiversity was recovering from recent disturbance. Reanalysis of this question in the future would be valuable.

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 further on). Our reanalyses 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

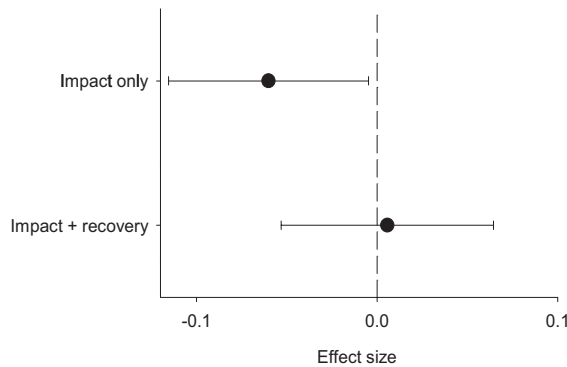


FIG. 5. Reanalysis of the data from Vellend et al. The original dataset included two types of studies – those showing how local richness is affected by some driver (impact) and those focused on how richness recovers following effects of a driver (recovery). We reanalyzed effect sizes in the Vellend et al. dataset (the LRR of mean richness in final vs. initial surveys) using a mixed model ANOVA with ‘STUDY’ included as a random effect and observations weighted by square root of sample size (as the authors did). The effect sizes are calculated using both types of studies and with studies assessing direct impact only.

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

Despite these conflicting results and past criticisms (Cardinale 2014, Isbell et al. 2015), McGill et al. (2015) recently claimed: “There is considerable empirical evidence that continental biodiversity at regional or local scales is also holding steady or increasing ... recent analyses that collectively assembled published data from hundreds of biodiversity inventory studies found that local diversity is, on average, constant.” This statement does not reflect the balance of evidence on local biodiversity change in the Anthropocene, and is one side of a debate that not only has yet to be resolved, but which has the potential to influence the support of policy-makers for conservation, strategies used by managers to preserve or restore biodiversity, and the priorities set by funding agencies and journals. Because the conservation

stakes of this debate are high, we would like to highlight three lessons that we have taken from recent attempts to quantify biodiversity change.

A Caution

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

A striking example of overextending conclusions from meta-analysis is apparent in Vellend et al. (2013), who framed their paper as a critique of biodiversity and ecosystem functioning research. Their finding of no net change in local diversity was used to argue that “the clear lack of any general tendency for plant biodiversity to decline at small scales in nature directly contradicts the key assumption linking experimental results to ecosystem function as a motivation for biodiversity conservation in nature” (Vellend et al. 2013). This argument is illogical, however, because it confuses variables and spatial scales. Vellend et al. (2013) pooled studies of changing species richness (variable Y) across a disparate set of sites and taxonomic groups that underwent gains and losses in local biodiversity due to opposing processes (variables X); decreases in biodiversity following perturbations (e.g., fires, grazing, volcanic eruption) and increases in biodiversity as communities were recovering from perturbations. First, finding no average change over these times series is not evidence that local biodiversity change does not affect a third local variable (Z)—ecosystem functioning—which was not measured or included in their dataset. Second, it is not the global average of these changes that matter for many ecosystem properties, which are driven by the species present in the local communities. BEF experiments control levels of species richness because they change locally for many reasons (Wardle et al. 2011)—as is clear from the distribution of response ratios in the Vellend et al. (2013) dataset.

Unequivocal inference about the cause of biodiversity changes requires experiments that control the degree of human impact (e.g., Haddad et al. 2015). The meta-analyses of Vellend et al. (2013) and Dornelas et al. (2014) did not include data from controlled experiments. Whole-ecosystem manipulations with Before-After Control-Impact (BACI) analyses and their extensions (Underwood 1994) are designed to deal with the difficulties of detecting change and attributing the cause of change when short time-series are obtained from unreplicated systems.

Rather than ignore experimental evidence, it should be an essential part of meta-analytic approaches to defining the expectations for the sign and magnitude of local biodiversity change.

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

A need

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

Biodiversity is a fundamental property of the planet's ecosystems and should be systematically monitored. To do this, monitoring programs need to be spatially and temporally representative across the globe (Scholes et al. 2008). The first step towards this goal would be to complete a formal "gap analysis," which would probably identify what most of us already recognize, and which we present here—we need monitoring programs that extend beyond the borders of the U.S. and Europe, and that capture biomes that are strongly underrepresented in current biodiversity datasets, such as the tropics, boreal forests, the tundra, and deserts on land, the ocean benthos, and the Indian Ocean and Indo-Pacific Oceans, which harbor large fractions of marine diversity. After formalizing the gaps and needs, the second step will be for international organizations like IPBES (<http://www.ipbes.net/>) to urge the development of better biodiversity monitoring programs. New initiatives like GEO BON (Scholes et al. 2008, <http://geobon.org/>) are taking the first

important steps towards establishing a group of biodiversity observation networks around the globe, but the funding needed to organize and sustain efforts in poor and developing countries is chronically lacking. Technological innovations may complement research networks by allowing individual experts or citizen scientists to track and monitor biodiversity from any given location using their cell phones (e.g., Goldsmith 2015). Ultimately, these efforts may produce a lot of data with high taxonomic resolution for some species groups, but it will likely have limits in spatial, temporal and taxonomic resolution and scale. Therefore, new technologies that can monitor additional aspects of biodiversity with high spatial and temporal resolution will be important tools for truly representative monitoring of biodiversity (Asner et al. 2015, Pimm et al. 2015). If we progress to a set of monitoring programs with good spatial, temporal, and taxonomic resolution, and coordinated data collection, then we will be in a position to improve analyses of local biodiversity change (e.g., Azalee et al. 2015).

A challenge

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

ACKNOWLEDGMENTS

We would like to thank two anonymous reviewers for their helpful comments and suggestions that much improved the manuscript. We thank Patrick Thompson for help with R code. AG is supported by an NSERC Discovery grant, the Canada Research Chair Program and the Quebec Centre for Biodiversity Science. BJC is supported by NSF grant 1332342. DGB and GRHA are supported by the NASA Land Cover Land Use

Change Program (NNX14AD85G). JEKB is supported by MIT Seagrant 2014-R/RCM-36. ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). MO is supported by an NSERC Discovery Grant and a Sloan Foundation Ocean Sciences Fellowship.

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