

Recent Trends in Local-Scale Marine Biodiversity Reflect Community Structure and Human Impacts

Highlights

- Recent temporal change in marine biodiversity was context dependent
- Local net gain of species was the prevailing signal in our dataset
- Biodiversity change depended on human impacts, community structure, and spatial scale
- Long-term monitoring sites are unlikely to be a random sample of the global ocean

Authors

Robin Elahi, Mary I. O'Connor,
Jarrett E.K. Byrnes, Jillian Dunic,
Britas Klemens Eriksson,
Marc J.S. Hensel, Patrick J. Kearns

Correspondence

elahi@stanford.edu

In Brief

Elahi et al. use a global synthesis of marine time series to demonstrate that local biodiversity change in recent decades depended on human impacts, community structure, and spatial scale. A synthetic understanding of local biodiversity trends is incomplete without information on local ecological conditions.

Recent Trends in Local-Scale Marine Biodiversity Reflect Community Structure and Human Impacts

Robin Elahi,^{1,2,*} Mary I. O'Connor,² Jarrett E.K. Byrnes,³ Jillian Dunic,³ Britas Klemens Eriksson,⁴ Marc J.S. Hensel,³ and Patrick J. Kearns³

¹Hopkins Marine Station, Stanford University, Pacific Grove, CA 93940, USA

²Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

³Department of Biology, University of Massachusetts, Boston, MA 02125, USA

⁴Department of Marine Benthic Ecology and Evolution, Centre for Ecological and Evolutionary Studies, University of Groningen, Nijenborgh 7, 9747 AG Groningen, the Netherlands

*Correspondence: elahi@stanford.edu

<http://dx.doi.org/10.1016/j.cub.2015.05.030>

SUMMARY

The modern biodiversity crisis reflects global extinctions and local introductions. Human activities have dramatically altered rates and scales of processes that regulate biodiversity at local scales [1–7]. Reconciling the threat of global biodiversity loss [2, 4, 6–9] with recent evidence of stability at fine spatial scales [10,11] is a major challenge and requires a nuanced approach to biodiversity change that integrates ecological understanding. With a new dataset of 471 diversity time series spanning from 1962 to 2015 from marine coastal ecosystems, we tested (1) whether biodiversity changed at local scales in recent decades, and (2) whether we can ignore ecological context (e.g., proximate human impacts, trophic level, spatial scale) and still make informative inferences regarding local change. We detected a predominant signal of increasing species richness in coastal systems since 1962 in our dataset, though net species loss was associated with localized effects of anthropogenic impacts. Our geographically extensive dataset is unlikely to be a random sample of marine coastal habitats; impacted sites (3% of our time series) were under-represented relative to their global presence. These local-scale patterns do not contradict the prospect of accelerating global extinctions [2,4,6–9] but are consistent with local species loss in areas with direct human impacts and increases in diversity due to invasions and range expansions in lower impact areas. Attempts to detect and understand local biodiversity trends are incomplete without information on local human activities and ecological context.

RESULTS AND DISCUSSION

Near-shore marine environments harbor a wealth of biodiversity [12] and provide valuable ecosystem services to humans [13].

They also have served as a testing ground for theory on the regulation and maintenance of species diversity [14–18]. Yet, little of the recent analysis of local biodiversity trends has included coastal communities or the processes known to influence diversity and temporal stability [10,11,19,20]. In coastal marine ecosystems around the globe, we detected increases in the number of species (species richness) and diversity (Shannon index, H'), a metric that considers species' relative abundances (Figures 1 and S1). This general increase in local-scale biodiversity contrasts with recent findings in terrestrial systems and other global syntheses [10,11], as well as the prevailing trend of species loss at the global scale [2,4,6–9].

The overall positive trend in the richness dataset was reflected most strongly in 16% of richness time series, which displayed significantly positive trends (see *Supplemental Experimental Procedures*). In contrast, only 3% of time series displayed significant declines in richness. Net species gains were likely to be strongly mediated by indirect effects of increased abundance [21] because total abundance of individuals was a very important predictor of species richness (Table S1). Another mechanism consistent with gains in richness is an increase in the abundance of historically present but rare species relative to common species. Indeed, increased relative abundances of previously uncommon species was reported in one of the most temporally intensive and spatially thorough monitoring programs included in our synthesis [22].

Despite the overall trend of local species gain, we observed large variation in the strength and even the direction of the trend among time series (Figures 1 and S1). Notably, the observed variation was consistent with predictions derived from ecological theory for how local diversity might be expected to change through time (Table 1). Temporal change in species richness depended on ecological context: removing all five hypothesized ecological predictors (spatial scale, anthropogenic drivers, trophic level, initial richness, and length of time series) on temporal variation in richness resulted in very poor models (Table S1). Predictable variation among time series demonstrates that information on local events and conditions is required to understand the direction (sign) and magnitude of local biodiversity change in recent decades.

Proximate human activities partially explained the direction and magnitude of species diversity change. In our dataset, net species loss was evident in the few ($n = 9$) time series associated

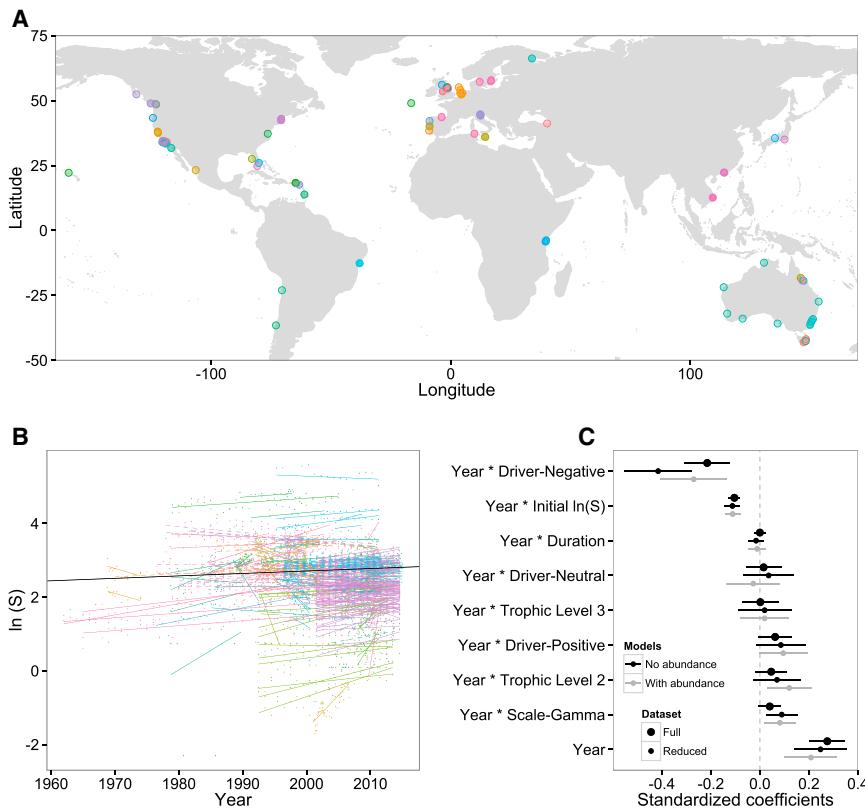


Figure 1. Global Distribution of the Sites in the Present Synthesis and Temporal Change in Species Richness in the Context of Hypothesized Ecological Predictors

(A) Distribution of the 189 study sites in our synthesis. Time-series data were compiled from 57 unique studies, represented by different colors. Dots are semitransparent, such that darker colors indicate overlap of multiple sites.

(B) Each line represents the ordinary least-squares slope for a single time series. Solid lines designate time series ($n = 220$) with abundance data, and dashed lines designate time series ($n = 82$) without abundance data. The black line represents the predicted mean intercept and slope of the relationship between species richness and time based on a hierarchical, linear mixed model testing the effect of year on richness, with random intercepts and slopes for each time series (see [Supplemental Experimental Procedures](#)). In this study, we were interested primarily in whether the slope term was necessary for model fit (i.e., has richness changed over time?). Colors represent the unique studies and match the colors in panel (A).

(C) The standardized coefficients of ecological predictors and their 95% confidence intervals for the full dataset (large black points) and the reduced dataset (small black and small gray points, respectively). The reduced dataset contained only time series with both richness and abundance (see [Experimental Procedures](#)). We include standardized coefficients for two sets of models for the reduced dataset: one with the models that also included abundance as a predictor

same set of candidate models as the full dataset (small black points) and the second with a set of candidate models (see [Table S1](#)). The sizes of points representing full and reduced datasets are scaled relative to their number of observations.

See also [Figures S1](#) and [S2](#) and [Table S1](#).

with local anthropogenic stressors predicted a priori to have negative consequences for biodiversity ([Figures 1C](#) and [2C](#)), such as pollution and sedimentation. In contrast, sites that were associated with local anthropogenic drivers predicted to increase biodiversity (e.g., artificial reef restoration, cessation of pollution) predominantly experienced net species gains. Surprisingly, sites that were not identified a priori as experiencing an unambiguous positive or negative anthropogenic driver displayed, on average, net species gains over time. However, these gains

were smaller in magnitude in comparison to sites where human influences were predicted to exert positive influences on biodiversity. Although there is no evidence of publication bias in our dataset overall ([Figure S2](#)), we cannot rule out the possibility that studies demonstrating richness declines associated with explicit anthropogenic drivers may have been more likely to be published. More work on human impacts is sorely needed, but our analysis is proof of concept that their consideration is essential to understanding global trends in local biodiversity change.

Table 1. Hypotheses and Associated Predictions Related to Temporal Change in Biodiversity that Were Tested Explicitly in Our Study

Hypotheses	Predictions
Local anthropogenic drivers influence the trajectory of change in richness	beneficial drivers (e.g., artificial reef restoration, fishing closures) will be associated with positive temporal change in richness, whereas detrimental drivers (e.g., pollution, anthropogenic structures) will be associated with negative temporal change in richness [20]
Species range expansions and introductions increase richness over time	temporal change in richness will be greater at the gamma (e.g., site) scale than the alpha (e.g., plot) scale [1,23] temporal change in richness will be positive for lower trophic levels and negative for higher trophic levels (trophic skew hypothesis) [24,25] temporal change in richness will be larger for time series that have a low initial richness (diversity-invasion resistance hypothesis) [26,27] temporal change in richness will be larger for time series that have a high initial richness (rich get richer hypothesis) [28,29]
Turnover occurs but no net change in richness	in the absence of changes to productivity and the regional species pool, environmental changes affect composition, but not richness [30]

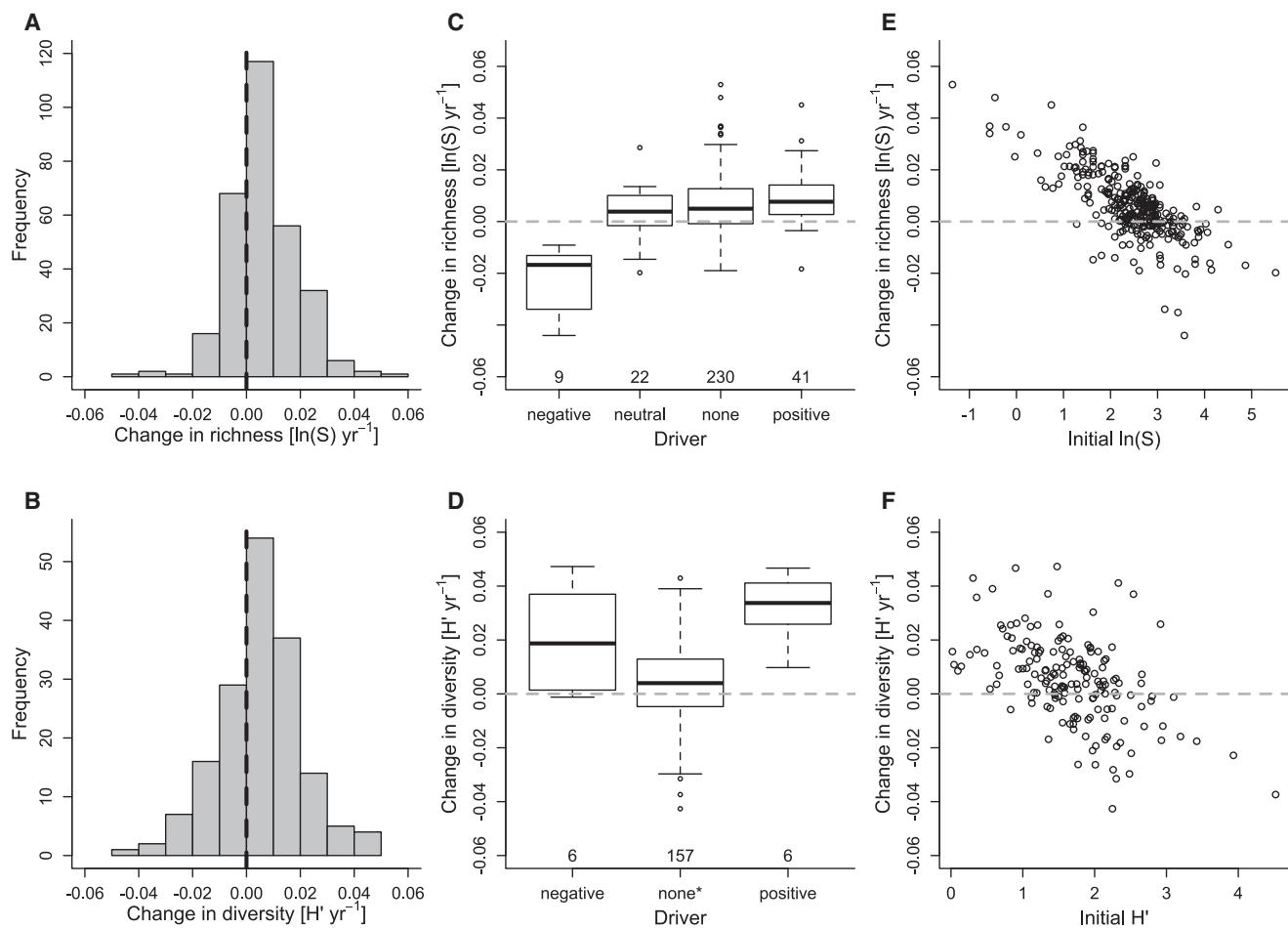


Figure 2. Temporal Change in Biodiversity Was Modified by Anthropogenic Impacts and the Initial Biodiversity of the Community

(A and B) Frequency distribution of temporal change in species richness (A) and Shannon diversity (B). (C–F) Temporal change in biodiversity depended on localized anthropogenic drivers (C and D) and the initial biodiversity (E and F) of the community. Time series associated with detrimental drivers (e.g., pollution) were predicted to exhibit negative trajectories, while time series associated with beneficial drivers (e.g., reef restoration) were predicted to exhibit positive trajectories. The classification of some drivers (e.g., warming) as negative or positive was equivocal and thus classified as neutral. Most time series were not explicitly associated with a driver ("none"). For Shannon diversity (D), only one time series was classified as "neutral" but for analysis was treated as "none." Temporal change was estimated for each time series as the fitted slope from hierarchical mixed models, taking into account all of the predictors of interest (i.e., the full model; see [Experimental Procedures](#)). Boxplots display the median and interquartile range (IQR) of data, with outliers plotted as circles beyond whiskers when the values are $1.5 \times$ IQR from the first or third quartile.

See also [Tables S1](#) and [S2](#).

The patterns associated with negative human impacts differed for species richness and Shannon diversity. This reinforces the notion that different biodiversity metrics may not exhibit parallel responses to environmental change due to the inherent complexity of compositional shifts in species [19,31]. Our analysis indicated that communities exhibited decreases in richness but stable, or increasing, Shannon diversity in the context of negative drivers, perhaps through the loss of rare species. However, communities associated with positive drivers exhibited larger gains in Shannon diversity than richness, suggesting that the recovery of species already in the community increased evenness. These conclusions remained unchanged when considering only time series for which both richness and Shannon diversity data were available. Given the small number of studies exhibiting negative drivers, we tested whether our con-

clusions were highly sensitive to errors in the classification of drivers ([Table S2](#)) using a randomization procedure ([Supplemental Experimental Procedures](#)). We found that our conclusions regarding human impacts were robust to classification errors of 32% and 54% for richness and diversity, respectively ([Figure S2](#)).

Attributes of the species assemblage also explained variation in how biodiversity changed through time. Species-poor sites and assemblages comprised mainly of species lower in the food web (e.g., suspension feeders; [Table S3](#)) gained a disproportionate number of species. These observations are consistent with a signal of species invasions in coastal ecosystems [24,32]. Local communities with many species are thought to better resist invasion by novel species through the preemption of resources [26,27]. In accordance with

this “diversity-invasion resistance” hypothesis, species-poor communities exhibited the greatest temporal increases in richness, while sites with high initial richness exhibited little net change and some species losses over time (Figure 2E). A similar but weaker pattern was observed for Shannon diversity (Figure 2F). There are at least two plausible alternatives to the diversity-invasion resistance hypothesis. First, increases in richness in species-poor systems are also consistent with recovery from historical disturbance that could have reduced diversity prior to initiation of the time series and suggests that identifying the proper “baseline” for assessing net change in biodiversity is difficult [33]. Second, the signal of species gains in depauperate communities may reflect the stochastic nature of dispersal limitation. In the context of reduced dispersal limitation for some cosmopolitan species (e.g., through ballast water transport) [32], colonizers are more likely to represent novel species in depauperate communities (by chance alone) and thus contribute to the inverse relationship between biodiversity change and initial biodiversity. Disentangling the relative importance of these mechanisms will necessarily be a local endeavor.

We detected stronger increases in species richness at the site (i.e., gamma) scale compared to the sample scale (Figure 1C, Table S1). These observations are consistent with a niche-based framework for biological invasions [23], where species interactions limit colonizers at the sample scale but habitat heterogeneity promotes colonizers at larger scales. However, variation in detection of changes in biodiversity with scale could also reflect scale-dependent sampling biases [34]. For example, the effect of scale in our analysis may also be related to the detectability of new, uncommon species in sampling units versus sites. That is, a colonizing species need only be present in one plot to affect site-scale richness estimates without necessarily increasing average sample-scale richness.

Our findings beg explanation of how these patterns can be reconciled with the vast evidence for a modern crisis of global biodiversity loss. One explanation for the observed positive biodiversity trends is that our dataset and the thousands of observations comprising two other recent data syntheses [10, 11] are not random samples of the planet. Thus, it is unlikely that they are completely representative of patterns of local biodiversity change worldwide. Many of the datasets in our study represent long-term observations initiated decades ago to study the natural history of ecological communities. To study natural processes, scientists often choose sites where human activities are perceived to be minimal to avoid confounding natural and anthropogenic signals. These sites would be predicted to be the least likely to experience diversity loss from human activities but still may be subject to increases due to regional species invasions.

Most time series in our dataset (76% for richness) fell into the category of no explicitly observed human impact (“none”; Figure 2) and could not be associated *a priori* with a clear local driver of net species loss or gain. Therefore, our dataset could overrepresent relatively well-preserved sites but underrepresent heavily polluted or modified sites. We suggest that this bias in the available coastal marine time series data is likely true of other recent syntheses of biodiversity change and warrants further exploration before accurate global trends in local-scale biodiversity change become clear.

We compared the bias in our dataset against quantified cumulative human impacts in the ocean. The percentage of the global ocean experiencing at least “medium-high” human impacts (>50% degraded, sensu [35]) is over 40%, and the percentage for coastal systems is likely to be even higher. Estuaries and urbanized areas are typically considered to be heavily impacted habitats, and 13% of the richness time series in our dataset were conducted in these habitats. Even more striking, only 3% of richness time series came from areas associated with decidedly negative drivers. In contrast, 18% of studies were conducted in protected areas or parks (relative to an estimated 3% of protected global ocean [36]). Admittedly simple, these comparisons suggest that the availability of studies for our synthesis was likely biased toward less-impacted sites. It is very possible that species losses at local scales have occurred over much longer periods and are more prevalent than could be detected by our dataset, warranting caution when considering the body of evidence on local biodiversity change to which our study is but one contribution.

Still, we observed a prevailing positive signal of biodiversity change, rather than one of stability, in the absence of clear local drivers. It is plausible that global loss of species is complemented at the finest scales (<1 to hundreds of meters) by species gains through a variety of mechanisms. The signal of species introductions is likely to be strong in our dataset because coastal communities are prone to the pervasive effects of human-assisted transport of marine life [24,32]. Species gains were weak for consumers and predators (Figure 1C), who tend to be large and are often the direct or indirect targets of harvesting [9]. In contrast, species gains were strongest for benthic invertebrates, consistent with the observation that most non-native species in coastal marine systems are suspension-feeding invertebrates [24,25]. Further, nearly all coastal areas have warmed since 1960 [37]. The influx of thermal niches from adjacent regions has likely facilitated species range expansions [38–40] and the addition of novel species to local communities, as well as increases in the abundance of historically present but uncommon species [22, 41].

Inferences about biodiversity trends depend critically on the duration and timing of sampling [42], raising the possibility that the initial richness of communities sampled recently has already been modified by past extinctions and immigrations (i.e., sliding baselines; [33]). In contrast, the contemporary balance of biodiversity may not yet reflect time lags in the eventual extinction of species due to habitat destruction and/or overexploitation (i.e., extinction debt; [2]), or on delays in the arrival of new species (i.e., immigration credit; [42]). Although our analysis indicated that study duration was not statistically relevant, approximately two-thirds of the richness data were compiled from time series shorter than 15 years. To address concern that the overall positive trend in richness over time was driven by these short studies, many of which began after 2000 (Figure 1B), we reanalyzed our data excluding studies shorter than 15 years. The overall trend of species gain remained but was weaker (see *Supplemental Experimental Procedures*). This observation warrants caution when interpreting biodiversity change from short time series.

The spatial, temporal, and human impact biases in this biodiversity time series synthesis reflect the availability of data that

were collected in the past and are likely common to other time series syntheses. These biases—when considered carefully—do not diminish the strength of our conclusions. Despite an overall positive increase in local marine species richness over the last five decades, we found strong evidence for context dependence related to anthropogenic stressors, local biodiversity, spatial scale, and trophic level. Though this pattern differs from recent findings of no net change in local species richness [10,11], it is consistent with a general understanding of how ecosystems respond to intense perturbations [1–3]. Further, when human-mediated disturbances are considered explicitly, declines in species richness are common in terrestrial ecosystems [20]. Our results suggest that local-scale biodiversity change might be predictable, and therefore manageable, given knowledge of relevant drivers and the ecological processes that relate local species diversity to regional and global change.

It is clear that the wholesale conversion of natural ecosystems for the purposes of agriculture, aquaculture, and urban development directly and indirectly threatens biodiversity. However, in ecosystems that have not been transformed, and at very fine (local) scales at which ecologists often work, our results indicate that local changes in species diversity through species additions as well as losses are a reality, presenting challenges for biodiversity-oriented management. Conclusions about future biodiversity trajectories at local scales should explicitly quantify the prevalence and history of human impacts that may increase versus decrease biodiversity alongside considerations of the community itself: the number of species, trophic level, and spatial scale. This is a tall order, but our results suggest that once we understand these relevant factors, there is some hope for making predictions for the future of biodiversity at local scales.

EXPERIMENTAL PROCEDURES

To estimate recent trends in coastal marine biodiversity, we synthesized 471 time series datasets from 189 sites across the globe (Figure 1A) into a single, new database (Table S4). We focused on coastal biodiversity at the scale of species interactions (local scale; defined here as <1 to hundreds of meters), quantified as richness (S) and Shannon diversity (H'). These metrics differ in the information they convey about rare and common species. Changes in species richness reflect gains and losses in rare and common species equally. Shannon diversity further conveys information on the relative abundance of species such that an increase in diversity reflects both species number and the evenness of species' relative abundances. We included these two metrics because they were most frequently reported in the literature. In total, diversity metrics were obtained from 41 peer-reviewed publications and 9 unpublished reports, and they were calculated from 7 presence-absence or abundance matrices. Despite its frequent use by ecologists, we acknowledge that the Shannon index is sensitive to sampling effort and can be difficult to interpret because changes in H' can arise from changes in richness, evenness, or both [43].

We used hierarchical mixed-effects models (see *Supplemental Experimental Procedures*), model selection, and model averaging to answer three primary questions with our dataset: (1) Has marine biodiversity changed at local scales in recent decades? (2) Can we ignore the ecological context of biodiversity change? (3) Does the rate of biodiversity change depend on specific predictors in accordance with our a priori hypotheses (Table 1)? Our goal was not to find the “true” model but rather the best subset of a small set of candidate models testing explicit predictions, following the philosophy of Burnham and Anderson [44]. To address questions (1) and (2), we used a set of three nested models to tease apart the importance of year from the interaction between year and a set of five fixed predictors on richness. Next, to address question (3), our set of candidate models included the saturated

model and nested models without interactions between year × predictors for the full and reduced datasets (see *Supplemental Experimental Procedures*). With this approach, predictors were deemed ecologically relevant if their removal (e.g., the term year × scale) resulted in a poorer model based on information criteria (see below). Because species richness can vary as a consequence of variation in the total abundance of individuals sampled, we included abundance for a subset of the time series (“reduced dataset”) when such data were available, in a separate set of candidate models. Finally, we tested whether there was an overall effect of time on richness by including a model with the effect of year only (and random effects) and a null model (random effects only).

Candidate models were compared using the Akaike information criteria (AIC), a metric that considers both maximum likelihood scores and complexity (i.e., number of parameters, K). The difference in AIC (ΔI) between each model and the best model (i.e., lowest AIC) was calculated to emphasize the most plausible models given the data. Akaike weight (w_i), or the relative likelihood of each model, was obtained by normalizing the likelihood across the entire set of candidate models. We ranked models based on w_i and selected the set of models such that the cumulative sum was ≥ 0.9 , representing our 90% confidence set [44]. We then used model averaging to get the best estimates of parameters for the confidence set of models. Maximum likelihood was used for model selection, and restricted maximum likelihood was used for model averaging. Model fit was assessed using plots of standardized residuals against fitted values.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, and four tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.05.030>.

AUTHOR CONTRIBUTIONS

R.E., M.I.O., and J.E.K.B. conceived the study. All authors contributed to the collection of biodiversity datasets. R.E. assembled the database and analyzed data. R.E. and M.I.O. wrote the initial draft of the manuscript. All authors revised the manuscript.

ACKNOWLEDGMENTS

We would like to thank all of the researchers who contributed data, including C. Birkeland, E. Duffy, P.J. Edmunds, and K.P. Sebens. We thank D. Acuña, A. Honig, T. Ingty, and A. Wilson for assisting with the published literature search. A preliminary draft of the manuscript benefitted from discussions with G. De Leo, E. Aalto, F. Ferretti, and S. Sokolow; the final draft received excellent comments from three anonymous reviewers. The National Science Foundation provided funding for the preparation of this manuscript (DBI-1308719 to R.E.) and for the collection of biodiversity time series data (DEB 03-43570, 08-41441, and 13-50146 to P.J. Edmunds; OCE 0850809 and DGE 0742559 to K.P. Sebens). J.D. and M.J.S.H. were supported by MIT SeaGrant 2014-R/RCM-36. We acknowledge the following agencies for providing publicly available data: National Park Service (<http://pyrifera.marinemap.org/>), Long-Term Ecological Research Network (<http://mcr.lternet.edu/vinp>; <http://sbc.lternet.edu/>), and the Integrated Marine Observing System (IMOS; <https://imos.aodn.org.au/imos123>). IMOS is supported by the Australian government through the National Collaborative Research Infrastructure Strategy and the Super Science Initiative.

Received: January 21, 2015

Revised: April 6, 2015

Accepted: May 13, 2015

Published: July 9, 2015

REFERENCES

1. Sax, D.F., and Gaines, S.D. (2003). Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* 18, 561–566.

2. Tilman, D., May, R.M., Lehman, C.L., and Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature* 371, 65–66.
3. Vitousek, P.M., Mooney, H.A., Lubchenco, J., and Melillo, J.M. (1997). Human domination of earth's ecosystems. *Science* 277, 494–499.
4. Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
5. Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., and Collen, B. (2014). Defaunation in the Anthropocene. *Science* 345, 401–406.
6. Harnik, P.G., Lotze, H.K., Anderson, S.C., Finkel, Z.V., Finnegan, S., Lindberg, D.R., Liow, L.H., Lockwood, R., McClain, C.R., McGuire, J.L., et al. (2012). Extinctions in ancient and modern seas. *Trends Ecol. Evol.* 27, 608–617.
7. Dulvy, N.K., Sadovy, Y., and Reynolds, J.D. (2003). Extinction vulnerability in marine populations. *Fish Fish.* 4, 25–64.
8. McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., and Warner, R.R. (2015). Marine defaunation: animal loss in the global ocean. *Science* 347, 1255641.
9. Jackson, J.B.C. (2008). Colloquium paper: ecological extinction and evolution in the brave new ocean. *Proc. Natl. Acad. Sci. USA* 105 (1), 11458–11465.
10. Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., De Frenne, P., Verheyen, K., and Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci. USA* 110, 19456–19459.
11. Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., and Magurran, A.E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299.
12. Gray, J.S. (1997). Marine biodiversity: patterns, threats and conservation needs. *Biodivers. Conserv.* 6, 153–175.
13. Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., and Silliman, B.R. (2011). The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 169–193.
14. Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.* 100, 65–75.
15. Witman, J.D., Etter, R.J., and Smith, F. (2004). The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proc. Natl. Acad. Sci. USA* 101, 15664–15669.
16. Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
17. Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am. Nat.* 112, 23–39.
18. Karlson, R.H., Cornell, H.V., and Hughes, T.P. (2004). Coral communities are regionally enriched along an oceanic biodiversity gradient. *Nature* 429, 867–870.
19. Supp, S.R., and Ernest, S.K.M. (2014). Species-level and community-level responses to disturbance: a cross-community analysis. *Ecology* 95, 1717–1723.
20. Murphy, G.E.P., and Romanuk, T.N. (2014). A meta-analysis of declines in local species richness from human disturbances. *Ecol. Evol.* 4, 91–103.
21. Gotelli, N.J., and Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
22. Beukema, J.J., and Dekker, R. (2011). Increasing species richness of the macrozoobenthic fauna on tidal flats of the Wadden Sea by local range expansion and invasion of exotic species. *Helgol. Mar. Res.* 65, 155–164.
23. Shea, K., and Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176.
24. Byrnes, J.E., Reynolds, P.L., and Stachowicz, J.J. (2007). Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 2, e295.
25. Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* 6, 680–687.
26. Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. USA* 101, 10854–10861.
27. Stachowicz, J.J., Fried, H., Osman, R.W., and Whitlach, R.B. (2002). Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* 83, 2575–2590.
28. Lonsdale, W.M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536.
29. Stohlgren, T.J., Barnett, D.T., and Kartesz, J.T. (2003). The rich get richer: patterns of plant invasions in the United States. *Front. Ecol. Environ.* 1, 11–14.
30. Brown, J.H., Ernest, S.K.M., Parody, J.M., and Haskell, J.P. (2001). Regulation of diversity: maintenance of species richness in changing environments. *Oecologia* 126, 321–332.
31. Warwick, R.M., Ashman, C.M., Brown, A.R., Clarke, K.R., Dowell, B., Hart, B., Lewis, R.E., Shillabeer, N., Somerfield, P.J., and Tapp, J.F. (2002). Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees Estuary, UK, associated with local and regional environmental events. *Mar. Ecol. Prog. Ser.* 234, 1–13.
32. Wonham, M.J., and Carlton, J.T. (2005). Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. *Biol. Invasions* 7, 369–392.
33. Dayton, P.K., Tegner, M.J., Edwards, P.B., and Riser, K.L. (1998). Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecol. Appl.* 8, 309–322.
34. Chase, J.M., and Knight, T.M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecol. Lett.* 16, 17–26.
35. Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., et al. (2008). A global map of human impact on marine ecosystems. *Science* 319, 948–952.
36. Deguignet, M., Juffe-Bignoli, D., Harrison, J., MacSharry, B., Burgess, N.D., and Kingston, N. (2014). 2014 United Nations List of Protected Areas. (Cambridge: UNEP-WCMC).
37. Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., et al. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334, 652–655.
38. Sorte, C.J.B., Williams, S.L., and Carlton, J.T. (2010). Marine range shifts and species introductions: comparative spread rates and community impacts. *Glob. Ecol. Biogeogr.* 19, 303–316.
39. Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., et al. (2013). Global imprint of climate change on marine life. *Nat. Clim. Chang.* 3, 919–925.
40. Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669.
41. Green, D.H., Edmunds, P.J., and Carpenter, R.C. (2008). Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in cover. *Mar. Ecol. Prog. Ser.* 359, 1–10.
42. Jackson, S.T., and Sax, D.F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* 25, 153–160.
43. Magurran, A.E. (2004). Measuring Biological Diversity. (Oxford: Blackwell Science).
44. Burnham, K.P., and Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, Second Edition. (New York: Springer-Verlag).

Current Biology

Supplemental Information

Recent Trends in Local-Scale Marine Biodiversity

Reflect Community Structure and Human Impacts

**Robin Elahi, Mary I. O'Connor, Jarrett E.K. Byrnes, Jillian Dunic, Britas Klemens
Eriksson, Marc J.S. Hensel, and Patrick J. Kearns**

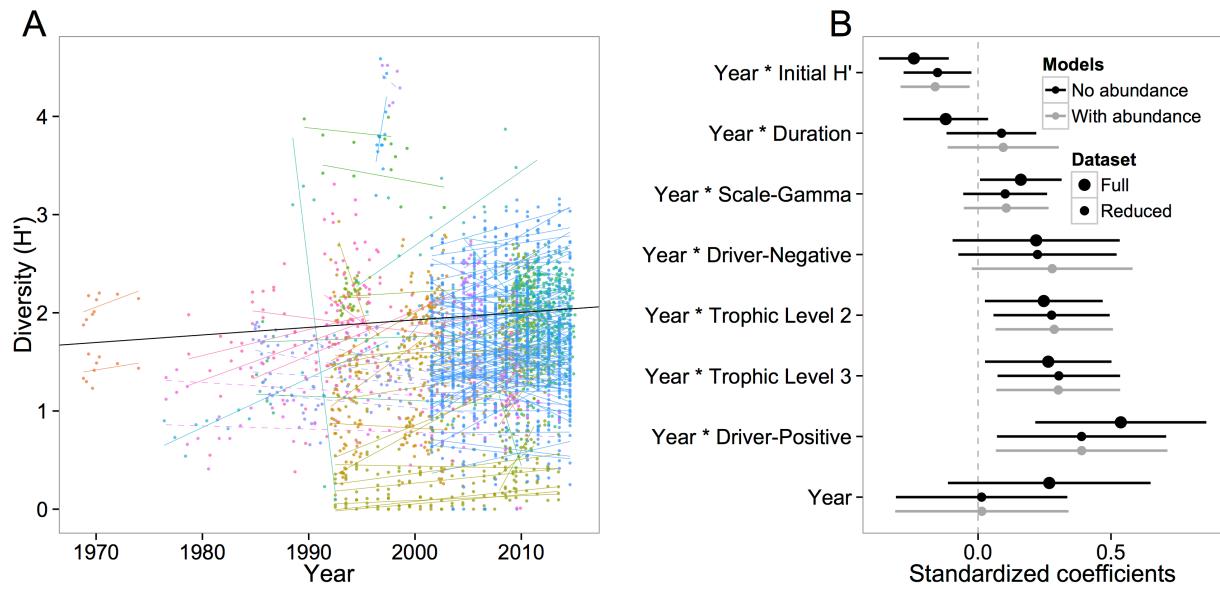


Figure S1 (Figure S1, Related to Figure 1 and Figure 2). Temporal change in Shannon diversity (H') and the influence of ecological predictors on temporal diversity change. In (A), each line represents the ordinary least squares slope for a single time series; colors correspond to unique studies. The black line represents the predicted mean intercept and slope of the relationship between Shannon diversity and time based on a hierarchical, linear mixed model testing the effect of year on richness, with random intercepts and slopes for each time series nested within site and study. In (B), the standardized coefficients of ecological predictors and their 95% confidence intervals for the full dataset (large black points) and the reduced dataset (small black and small gray points, respectively). The reduced dataset contained only time series with both richness and abundance (see Experimental Procedures). For the reduced dataset, we considered two sets of models: one with the same set of candidate models as the full dataset (small black points), and the second with a set of candidate models that also included abundance as a predictor (gray points, see Table S1). There were 2906 and 2586 observations for the full and reduced datasets, respectively. See also Table S1.

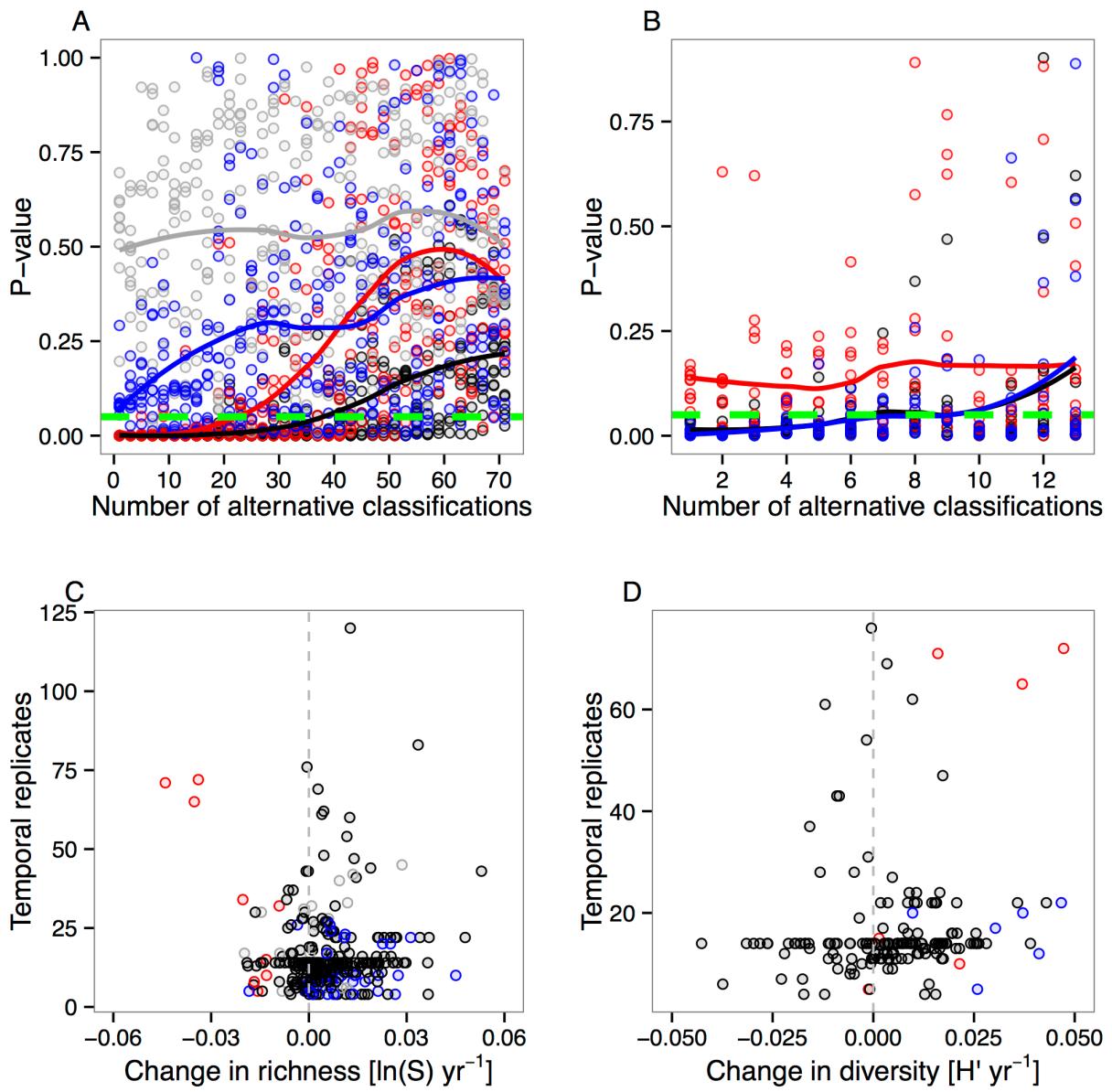


Figure S2 (Figure S2, Related to Figure 1, Figure 2, and Supplemental Experimental Procedures). Sensitivity analyses for the classification of time-series to anthropogenic drivers and funnel plots for the detection of publication bias. In (A), each point represents a p-value for the year \times driver effect from a global mixed effects model (with all five hypothesized predictors) from an individual simulation that randomly classified between 1 and 71 of the richness time-series as a negative, neutral, or positive driver (the remaining time-series, classified as having no

discernible driver, were not allocated randomly to a different driver). In (B), between 1 and 13 diversity time-series were reclassified as a negative, neutral, or positive driver. 10 simulations were performed for each level of alternative classifications. Solid lines are local polynomial regressions used to illustrate the sensitivity of the simulated p-values to alternative classifications. The green dashed line designates a statistical significance of 0.05. For (A) and (B), the different colors represent the three levels (blue, gray, and red for positive, neutral, and negative, respectively) and the overall (black) year \times driver effect. In the statistical model for richness, the reference level was ‘no anthropogenic driver’, and thus positive, neutral, and negative levels are plotted in (A). However, in the statistical model for diversity, the reference level was ‘neutral’, and thus only positive and negative levels are plotted in (B). In (C) and (D), the number of temporal replicates for each time-series is plotted against the fitted slope of species richness and Shannon diversity (against time), respectively. Neither funnel plot suggests evidence of publication bias, which would be the case if there were an absence of time-series (points) with small effect sizes (i.e., slopes) and low sample sizes (i.e., temporal replicates). The different colors represent the four levels of drivers (blue, gray, red, and black for positive, neutral, negative and none, respectively). See also Supplemental Experimental Procedures.

Table S1 (Related to Figure 1, Figure 2, Figure S1). Summary of model selection statistics from the linear mixed effects models for richness (S) and Shannon diversity (H'). For S and H', models tested the fixed effects of scale, driver, trophic level, initial biodiversity (S or H'), study duration (no. of years), and their interaction with year on biodiversity (S or H') for the full and reduced datasets. The reduced datasets only included time series for which abundance data were available. For the reduced datasets, standardized log(abundance) was included in one set of the models. Model results include the number of parameters (K), AIC, delta AIC (Δi), model likelihood, weighted model likelihood (w_i), log likelihood, and cumulative weights of the models. Models are arranged by ascending AIC. Models above the dotted line indicate the 90% confidence set of models. Terms that were removed in the models below this line were considered to be ecologically meaningful.

Table S1 (Related to Figure 1, Figure 2, Figure S1). See above for legend.

Model	K	AIC	Δi	Model likelihood	w _i	Log likelihood	Cumulative weight
<i>Richness; full dataset</i>							
W/O Year:Study Duration	24	1752.86	0	1	0.541	-852.43	0.54
Full model*	25	1754.66	1.8	0.406	0.22	-852.33	0.76
W/O Year:Trophic Level	23	1755.63	2.77	0.25	0.135	-854.82	0.9
W/O Year:Scale	24	1756.16	3.3	0.192	0.104	-854.08	1
W/O Year:Driver	22	1773.43	20.57	0	0	-864.72	1
W/O Year:Initial S	24	1818.48	65.62	0	0	-885.24	1
Year only	9	2406.16	653.3	0	0	-1194.08	1
Null model	8	2417.45	664.59	0	0	-1200.72	1
<i>Richness; reduced dataset</i>							
W/O Year:Study Duration	24	1695.36	0	1	0.449	-823.68	0.45
Full model*	25	1696.3	0.94	0.625	0.281	-823.15	0.73
W/O Year:Trophic Level	23	1696.58	1.22	0.544	0.244	-825.29	0.97
W/O Year:Scale	24	1701.1	5.74	0.057	0.025	-826.55	1
W/O Year:Driver	22	1726.01	30.66	0	0	-841.01	1
W/O Year:Initial S	24	1741.63	46.27	0	0	-846.81	1
Year only	9	2180.98	485.62	0	0	-1081.49	1
Null model	8	2194.12	498.76	0	0	-1089.06	1
<i>Richness; reduced dataset, abundance as predictor</i>							
W/O Year:Study Duration	25	946.19	0	1	0.531	-448.09	0.53
Full model**	26	946.74	0.55	0.76	0.403	-447.37	0.93
W/O Year:Scale	25	950.5	4.31	0.116	0.061	-450.25	1
W/O Year:Trophic Level	24	955.82	9.63	0.008	0.004	-453.91	1
W/O Year:Driver	23	960.52	14.34	0.001	0	-457.26	1
W/O Year:Initial S	25	992.31	46.12	0	0	-471.15	1
Year and abundance only	10	1420.15	473.96	0	0	-700.07	1
W/O Abundance	25	1696.3	750.11	0	0	-823.15	1
Null model	8	2194.12	1247.93	0	0	-1089.06	1
<i>Diversity; full dataset</i>							
W/O Year:Study Duration	23	2002.17	0	1	0.382	-978.09	0.38
Full model***	24	2002.37	0.2	0.905	0.346	-977.19	0.73
W/O Year:Trophic Level	22	2003.8	1.62	0.444	0.17	-979.9	0.9
W/O Year:Scale	23	2004.98	2.81	0.246	0.094	-979.49	0.99
W/O Year:Driver	22	2010.36	8.18	0.017	0.006	-983.18	1
W/O Year:Initial H'	23	2013.6	11.43	0.003	0.001	-983.8	1

Year only	10	2204.96	202.79	0	0	-1092.48	1
Null model	9	2210.68	208.51	0	0	-1096.34	1
<i>Diversity; reduced dataset</i>							
W/O Year:Study Duration	23	1790.68	0	1	0.419	-872.34	0.42
W/O Year:Scale	23	1791.74	1.07	0.587	0.245	-872.87	0.66
Full model***	24	1792.15	1.47	0.479	0.2	-872.07	0.86
W/O Year:Initial H'	23	1794.46	3.79	0.151	0.063	-874.23	0.93
W/O Year:Driver	22	1795.27	4.6	0.1	0.042	-875.64	0.97
W/O Year:Trophic Level	22	1795.91	5.24	0.073	0.031	-875.96	1
Year only	10	1974.79	184.12	0	0	-977.4	1
Null model	9	1984.59	193.91	0	0	-983.29	1
<i>Diversity; reduced dataset, abundance as predictor</i>							
W/O Year:Study Duration	24	1771.29	0	1	0.422	-861.64	0.42
W/O Year:Scale	24	1772.33	1.04	0.593	0.25	-862.16	0.67
Full model****	25	1772.67	1.39	0.5	0.211	-861.34	0.88
W/O Year:Initial H'	24	1775.35	4.07	0.131	0.055	-863.68	0.94
W/O Year:Driver	23	1776.49	5.2	0.074	0.031	-865.25	0.97
W/O Year:Trophic Level	23	1776.53	5.24	0.073	0.031	-865.26	1
W/O Abundance	24	1792.15	20.86	0	0	-872.07	1
Year and abundance only	11	1957.25	185.97	0	0	-967.63	1
Null model	9	1984.59	213.3	0	0	-983.29	1

* $\ln(S) \sim \text{Year}^*\text{Scale} + \text{Year}^*\text{Driver} + \text{Year}^*\text{Trophic Level} + \text{Year}^*\text{Initial S} + \text{Year}^*\text{Study Duration}$

** $\ln(S) \sim \text{Year}^*\text{Scale} + \text{Year}^*\text{Driver} + \text{Year}^*\text{Trophic Level} + \text{Year}^*\text{Initial S} + \text{Year}^*\text{Study Duration} + \text{Abundance}$

*** $H' \sim \text{Year}^*\text{Scale} + \text{Year}^*\text{Driver} + \text{Year}^*\text{Trophic Level} + \text{Year}^*\text{Initial H}' + \text{Year}^*\text{Study Duration}$

**** $H' \sim \text{Year}^*\text{Scale} + \text{Year}^*\text{Driver} + \text{Year}^*\text{Trophic Level} + \text{Year}^*\text{Initial H}' + \text{Year}^*\text{Study Duration} + \text{Abundance}$

Table S2 (Related to Figure 1, Figure 2, Figure S1). The number of studies and time series examining changes in richness (S) or Shannon diversity (H') that were associated with a potential driver of ecosystem change. We assigned each driver to neutral, negative, or positive predictions for the temporal trajectory of change in richness or diversity (see Supplemental Experimental Procedures).

Driver	Richness		Diversity	
	No. of studies	No. of time series	No. of studies	No. of time series
<i>No Prediction</i>	40	230	22	156
<i>Neutral Prediction</i>				
Hurricane (middle of time series)	1	1	0	0
Hurricanes	2	2	0	0
Red tide	1	3	0	0
Warming (local) from nuclear plant	3	5	1	1
Warming (regional) 1998 El Nino	5	10	0	0
Warming (regional) and invasion	1	1	0	0
<i>Total</i>	13	22	1	1
<i>Negative Prediction</i>				
Dike construction	1	1	1	1
Eutrophication	2	4	2	4
Hypoxia	1	1	1	1
Pollution	1	1	0	0
Sedimentation from nuclear plant	1	2	0	0
<i>Total</i>	6	9	4	6
<i>Positive Prediction</i>				
Artificial reef restoration	2	5	1	1
Eutrophication cessation	1	1	1	1
Fishing closure	5	24	0	0
Pollution cessation	4	11	2	4
<i>Total</i>	12	41	4	6

Table S3 (Related to Figure 1, Figure 2, Figure S1). The number of studies and time series examining changes in richness (S) or Shannon diversity (H') for a given taxon or group of taxa. We assigned the taxa from each study to trophic levels 1, 2 or 3 (see Supplemental Experimental Procedures).

Description of taxon	Richness		Diversity	
	No. of studies	No. of time series	No. of studies	No. of time series
<i>Trophic Level 1</i>				
algae	2	26	1	22
angiosperms	1	2	1	2
<i>Total</i>	3	28	2	13
<i>Trophic Level 2</i>				
benthic copepods	1	1	1	1
benthic invertebrates	16	47	6	16
benthic invertebrates and fish	1	1	1	1
coral	3	20	1	12
cryptobenthic fishes	1	1	1	1
flatworms	1	4	1	2
foraminifera	2	3	1	2
larval fish	1	1	1	1
pelagic copepods	1	1	0	0
sessile invertebrates	1	22	1	22
sessile invertebrates and flora	4	17	3	12
sponges	2	4	1	1
zooplankton	4	14	4	13
<i>Total</i>	38	136	22	62
<i>Trophic Level 3</i>				
benthic invertebrate and fish consumers	2	13	1	12
benthic invertebrate consumers	1	22	1	22
fish	17	103	4	27
<i>Total</i>	20	138	6	41

Table S4 (Related to Figure 1, Figure 2, Figure S1). Raw data, along with summary information, used in our study (provided as an excel file).

Supplemental Experimental Procedures

Data collection

We collected time series datasets that estimated richness (S), Shannon diversity (H'), or estimates of species abundance from which S and H' could be calculated (i.e., species abundance matrices). Criteria for inclusion were that the study (a) included measurements from at least four time points, (b) described a consistent sampling methodology (size and number of sampling units) through time, and (c) was considered to be “local-scale”. This last criterion depends on body size and the scales over which individuals interact. The largest areas included in our synthesis were on the order of thousands of square meters, for studies on reef fish populations (e.g., Channel Islands Kelp Forest Monitoring Project), while the smallest areas were quadrats of 10s of cm² for benthic invertebrates. We excluded studies that examined temporal change in richness across landscapes (e.g., the Nile delta, or the west coast of the United States). Studies presented richness estimates for species or the lowest distinguishable taxon; one study presented generic rather than species richness to avoid bias due to improvements in taxonomic identification over time [S1]. Similarly, we analyzed data from one database (IMOS; Integrated Marine Observing System) at the generic level. We obtained datasets by contacting principle investigators directly, searching online biodiversity databases, and conducting literature searches.

We searched the published and grey literature for studies that had resampled species richness or diversity over time by searching the Web of Science database and Aquatic Commons repository with the following search terms on February 19, 2014: (marine OR ocean* OR benthic* OR coral OR kelp* OR seamount OR vent OR mangrove OR “sea grass” OR seagrass OR plankton OR “deep sea” OR abyss* OR pelagic OR beach OR intertid* OR “salt marsh” OR “soft

“sediment” OR mudflat OR “mud flat” OR benthos OR “sub-tidal*” OR subtidal* OR “sub-littoral” OR sublittoral* OR macrobenthos OR estuar*) AND (biodiv* OR divers* OR richness OR evenness OR “community composition” OR “food web” OR “benthic communit*” OR [S2]“pelagic communit*”) AND (resurvey* OR resampl* OR “time series” OR “temporal change” OR decad* OR annual* OR multiyear OR “multi-year” OR “multi-decade” OR revisit*) NOT (fossil OR geologic* OR freshwater OR terrestrial OR grassland). This search returned 5785 references, which were filtered down to 41 publications and 9 unpublished reports according to the criteria above. Papers measuring bacterial species richness were excluded because of the ambiguity in resolving bacterial taxonomy.

Controlling for effects of variation in sampling effort and accuracy over time

We took several approaches to control for the potentially confounding effects of variation in sampling effort through time within studies. Occasionally, published studies and species abundance matrices did not report a consistent number of samples per time point, making the interpretation of richness trajectories problematic because they could be confounded by concurrent changes in sampling effort [S3]. For published studies, we removed individual time points with inconsistent sampling effort [e.g., S1], and in one case [S2], we separated the main study into two separate sub-studies (see below) to reflect two levels of sampling effort. For species abundance matrices, we found the minimum number of samples per time point, and randomly selected a subset of the minimum for all time points in the time series. Raw data and a complete description of the datasets used in this study are available (Table S4).

A problematic feature of monitoring studies is that the ability of observers to accurately identify taxa likely improves with experience, and thus an observed increase in richness through time may reflect improved researcher skill through time. We assume that many of these improvements occur during the early stages of monitoring. To minimize the potential for this bias, we inspected each of the original time series for qualitatively distinct and sudden increases in richness over the first several temporal observations. One study (Santa Barbara Coastal Long Term Ecological Research) exhibited sudden positive shifts and these early time points were removed prior to analysis. Our subjective approach cannot entirely eliminate bias, however, as it cannot identify gradual improvements over time.

However, published studies have used several strategies to minimize these biases, by using practiced and standardized underwater visual methods [S4, S5], using fixed species lists through time [S6], and analyzing generic, rather than species, richness [S1]. Even these latter two studies, which can be considered particularly conservative in their methodology, displayed clear increases in richness over the last two to four decades [S1, S6]. Indeed, an independent synthesis reported an increase in overall marine biodiversity at the local-scale, although the change was not significant [Figure S5 in S7].

In addition to sampling effort (size and number of samples), the number of observed individuals in a sample influences the number of observed species [S3]. In other words, the total abundance of individuals (e.g., fish), or the change in cover (e.g., benthic invertebrates), may change over time – and therefore a change in diversity is to be expected due to a sampling effect [S3]. Fortunately, abundance is often reported in studies of species richness, and one strength of our

analysis is that we incorporated abundance as a predictor in our hierarchical models (see below) for a subset of the database.

In total, we synthesized 471 richness and diversity time-series (spanning 1962-2015) from 189 sites across the globe (Figure 1A). Richness was compiled from 55 studies, 71 sub-studies, 302 time series, and 5073 observations (hereafter referred to as the ‘full richness dataset’). The subset of richness studies that also contained abundance information (hereafter referred to as the ‘reduced richness dataset’) comprised 40 studies, 52 sub-studies, 220 time series, and 3477 observations. The Shannon diversity dataset (hereafter referred to as the ‘full diversity dataset’) consisted of 26 studies, 33 sub-studies, 169 time series, and 2906 observations. The subset of diversity studies that also contained abundance information (hereafter referred to as the ‘reduced diversity dataset’) comprised 21 studies, 28 sub-studies, 156 time series, and 2586 observations. We were unable to calculate a complete number of observed species or occurrence records because these data were typically not reported in publications. In total, diversity metrics were obtained from 41 peer-reviewed publications, 9 unpublished reports (‘gray’ literature), and calculated from 7 presence/absence or abundance matrices (Table S4). Following the hypotheses outlined in Table 1, we articulated predictions for how biodiversity might change for each time series, based on potential drivers of ecosystem change (Table S2), spatial scale, trophic level (Table S3), and initial biodiversity.

Classification of studies by anthropogenic driver

For each time-series, we recorded any potential drivers of ecosystem change noted by the authors of published studies or principal investigators of unpublished studies. These included drivers

that were anticipated by the authors at the beginning of the study (e.g., fishing closure, eutrophication cessation), as well as drivers that were observed (but not anticipated) during the course of the monitoring program (e.g., species invasions, hurricanes). Each driver was grouped according to the following categories: hurricanes, red tides, seawater warming (local and regional), dike construction, eutrophication, hypoxia, pollution, sedimentation, artificial reef restoration, eutrophication cessation, fishing closures, and pollution cessation. We then classified each of these drivers as negative, neutral (i.e., uncertain), or positive drivers of biodiversity change. Most studies and time-series were not associated with any particular driver and classified as ‘none’ (Table S2). In general, time-series associated with anticipated drivers were readily assigned a ‘negative’ or ‘positive’ prediction of biodiversity change, but time-series experiencing unanticipated drivers were classified as ‘neutral’. For diversity, only one time-series was classified as neutral, and thus for the purposes of the statistical analysis (see below), was treated as ‘none’. The classification of anticipated drivers was based on *a priori* expectations stated by the authors of published studies and/or our interpretation and understanding of the ecological driver (e.g., we classified fishing closures as positive drivers of biodiversity change). Although seawater warming could be argued to be an anticipated driver of change, it does not unequivocally benefit or harm all species and thus predicting directional change in biodiversity is problematic.

We classified unanticipated drivers that were observed during the time-series as neutral for two primary reasons. First, it was not clear how to assign a prediction to unanticipated disturbances. For example, hurricanes and red tides might be expected to decrease diversity immediately (e.g., through indirect effects of reduced abundance) but display a recovery period indicative of

ecological succession. Therefore, the estimated trajectory of change (i.e., slope) depends on the timing of the sampling effort in relation to the pulse disturbance. Second, we did not wish to bias our analysis by including *post-hoc* explanations of biodiversity change. For example, if positive trends in biodiversity motivated an author to investigate specific mechanisms [e.g., species invasion; S6] that were supported by further examination of the data, we did not assign the driver to a positive prediction.

A primary consequence of our classification criteria was that the assigned negative and positive drivers of ecosystem change were very localized and anthropogenic in origin. Negative drivers included dike construction, eutrophication, hypoxia, pollution, and sedimentation. Positive drivers included reef restoration and the cessation of eutrophication, pollution, and fishing. A secondary consequence, due to the strict nature of our classification criteria, is that there were relatively few time-series with negative and positive drivers of change. In light of the extensive cumulative impacts documented for coastal oceans [S8], it is possible that we are underestimating human impacts in our synthesis. Nevertheless, we view our approach as an important first step towards understanding biodiversity change in the context of anthropogenic influences.

To evaluate the degree to which our classification affected our results and interpretation, we used a randomization procedure to assign alternative classifications to specific subsets of the 72 richness time-series that were associated with either a negative, neutral, or positive driver. Specifically, for a randomly chosen time-series (out of 72; not classified as ‘none’), we reassigned negative or positive drivers as neutral, and reassigned neutral drivers randomly to

either negative or positive. We then analyzed the modified data frame using the full mixed effects model and extracted p-values for the overall effect of prediction and the level-specific (i.e., negative, neutral, positive) p-values compared against the intercept (i.e., the ‘none’ category). We performed the randomization procedure 10 times for each of 1, 3, 5, 7...71 randomly selected time-series ($10 \times 36 = 360$ simulations). The resulting p-values were plotted against the number of switches to estimate visually the minimum number of alternative classifications needed to cause a shift in the interpretation of our results, using an alpha of 0.05 as an arbitrary cut-off point (Figure S2A). This approach suggested that at least 23 switches to the original classification scheme were needed to qualitatively change the interpretation of our results; i.e., changing the interpretation of negative drivers from being significantly different ($P < 0.05$) to being statistically indistinguishable ($P > 0.05$). Therefore, we consider the results and interpretation from our original classification of richness time-series to be relatively robust because it is unlikely that we misclassified ~32% of the 72 time-series. We performed a similar randomization procedure for the 13 diversity time-series ($10 \times 13 = 130$ simulations), and the results suggested that 7 alternative classifications (54%) were necessary to qualitatively change the statistical interpretation (Figure S2B).

Quantifying spatial scale

We considered explicitly the issue of scale by defining alpha and gamma scales of richness consistent with both classical [S9] and modern [S10] definitions of species diversity. Alpha richness referred to richness at the scale of the sampling unit (e.g., plot, transect, trawl, box core, etc), and the mean alpha richness was analyzed over time for a given site. Gamma richness referred to the total number of species across a number of samples, and often corresponded to

site-scale richness. For species abundance matrices (i.e., raw assemblage data), we calculated both alpha and gamma richness. We considered including sampling area explicitly in our models, but it was difficult to articulate a meaningful prediction for how sampling area would influence temporal change in biodiversity, given the heterogeneous distribution of organismal body sizes in our dataset. Although we don't include them explicitly as fixed effects, sampling area and body size are implicitly included in our models through the use of random effects (see below).

Classifying based on trophic level

We assigned each time series to one of three trophic levels, broadly representing primary producers (1), herbivores, deposit feeders, detritivores, and planktivores (2), and omnivorous consumers and carnivores (3). Our classification follows the designation of trophic levels in Byrnes et al. [S11], except that omnivorous consumers and carnivores were grouped into one level because no study focused solely on carnivores. When estimates of richness included taxa from two or more trophic levels we used the trophic level that was represented best by the sampling effort. For example, studies that examined fish were categorized as consumers and carnivores (trophic level 3) when herbivores, invertivores, and piscivores occurred together. Details are provided in Table S3.

Hierarchical classification

Observations in each time series were associated with information at three hierarchical levels. “Studies” consisted of single publications or original databases from a single, overarching research group (e.g., Santa Barbara Coastal Long Term Ecological Research). Within Studies,

“Sub-study” was used to designate groups typically pre-assigned by study authors, including taxa (e.g., algae, fish, invertebrates) and unique drivers (e.g., unprotected vs protected areas). Lastly, each “Time series” was associated with a specific Sub-study and a specific site.

Time Series Analysis

We used hierarchical mixed effects models to quantify temporal change in biodiversity in the context of specific predictors and random variation associated with studies. A strength of our approach is that it moves beyond calculating a single estimate of change (e.g., slope) for each time series and subsequently analyzing the frequency distribution of slope coefficients to infer patterns of change [S7, S12]. We were interested primarily in predicting the effect of time on richness (the coefficient, β), rather than richness itself (the intercept, α), according to the following model for log(richness) ($\ln(x + 0.1)$) of the i th observation:

$$\ln(S_i) = \alpha_{jkl[i]} + \beta_{l[i]} * \text{Year} + \varepsilon_i \quad \text{Eqn 1}$$

where ‘Year’ represents the number of years since the earliest temporal observation in our database, centered on the year 1990 [to improve model convergence; S13].

The linear mixed effects model estimates the variance associated with each nested random effect, namely study (j), sub-study (k), and time series (l). These random effects reflected the hierarchical nature of the data, but we were not interested in identifying the statistically optimal combination of random terms (e.g., through the use of information criteria) because (a) we identified an ecologically relevant set of random effects, (b) drawing inferences on random

effects can be problematic [S14], and (c) we did not wish to compare the full set (or subset) of candidate models in the interest of restricting our analyses to address the primary hypotheses (Table 1). We specified random intercepts for study and sub-study, and random slopes with correlated intercepts for each time series, for all of our models. Ecologically, this set of random effects quantifies the variance in average richness among studies, sub-studies and time series, as well as variance in the trajectory of change for each time series associated with unmeasured differences among datasets. Accounting for higher-level variance (i.e., site or sub-study) in slope terms was not considered to be of intrinsic ecological interest, and potentially redundant.

The fixed predictors of interest were related to (a) our hypotheses (driver, spatial scale, trophic level, initial richness) and (b) study level factors (duration). Therefore, for richness data, α and β can be represented by:

$$\alpha_{jkl|i} = \gamma_0 + \gamma_1 * Driver + \gamma_2 * Scale + \gamma_3 * Trophic Level + \gamma_4 * \ln(S_{initial}) + \quad \text{Eqn 2a}$$

$$\gamma_5 * Duration + \mu_j + \mu_k + \mu_l$$

$$\beta_{l|l} = \delta_0 + \delta_1 * Driver + \delta_2 * Scale + \delta_3 * Trophic Level + \delta_4 * \ln(S_{initial}) + \quad \text{Eqn 2b}$$

$$\delta_5 * Duration + \nu_l$$

$$\varepsilon_{jkl} \sim N(0, \sigma^2 \Lambda_{jkl})$$

with random intercepts (μ_j, μ_k, μ_l) and slopes (ν_l) normally distributed about zero with variance estimated by the model, as well as a correlation parameter between the slope and intercept for

time series (l). Due to the fact that biodiversity measured on dates closer together is likely to be more similar than biodiversity measured on dates further apart, we modeled the variance ($\sigma^2 \Lambda_{jkl}$) of within-group errors (ε_{jkl}) as an autoregressive correlation structure of order 1 (corAR1) [S15]. A continuous autoregressive correlation structure actually worsened model fit, and thus we used the simpler corAR1 for all of our analyses.

As with S, initial S was log transformed to improve homogeneity of residuals. Duration, like year, was centered on 1990 to improve model convergence. We considered including initial year as a predictor in our models, but it was strongly correlated with study duration. We chose to use study duration as a predictor in our models because it captures a general characteristic that is more broadly relevant given the relatively short temporal range of our dataset (1962 – 2015). Hierarchical models weight the influence of groups in part based on the number of observations, which might be expected to correlate with the duration of a study if longer studies include more observations than shorter studies. There was not, however, a strong relationship between duration and number of observations in our dataset.

For a subset of the richness data (hereafter referred to as the ‘reduced dataset’, as opposed to the ‘full dataset’), we were able to include abundance as a predictor of richness in our models by modifying equation 2a. Richness is often a saturating function of abundance, and thus we first log transformed abundance to linearize the relationship [S16, S17]. This modification introduced log abundance as a predictor of the intercept (B_0):

$$\alpha_{jkl[i]} = \gamma_0 + \gamma_1 * Driver + \gamma_2 * Scale + \gamma_3 * Trophic Level + \gamma_4 * \ln(S_{initial}) + \quad \text{Eqn 2c}$$

$$\gamma_5 * Duration + \gamma_6 * ln(Abundance) + \mu_j + \mu_k + \mu_l$$

We did not modify equation 2b, because it was not clear how abundance would influence the change in richness over time. Abundances from studies were recalculated (prior to log transformation) to conform to four common units, (a) percent cover, (b) individuals m⁻², (c) biomass m⁻² and (d) individuals m⁻³. Due to the heterogeneity, in type and scale, of these responses, we then normalized log abundances such that the mean abundance was 0 and variance was 1 within each time series [S18]. By accounting for abundance in our mixed effects models, we infer that any important predictors (as determined by AIC) drive temporal change in richness apart from the indirect effect of changes in density.

A similar set of models (with and without abundance) was used for the Shannon diversity dataset. The model was specified as follows:

$$H' = \alpha_{jkl[i]} + \beta_{l[i]} * Year + \varepsilon_{jkl} \quad \text{Eqn 3}$$

$$\alpha_{jkl[i]} = \gamma_0 + \gamma_1 * Driver + \gamma_2 * Scale + \gamma_3 * Trophic Level + \gamma_4 * H'_{initial} + \quad \text{Eqn 4a}$$

$$\gamma_5 * Duration + \mu_j + \mu_k + \mu_l$$

$$\beta_{l[i]} = \delta_0 + \delta_1 * Driver + \delta_2 * Scale + \delta_3 * Trophic Level + \delta_4 * H'_{initial} + \quad \text{Eqn 4b}$$

$$\delta_5 * Duration + \gamma_6 * ln(Abundance) + \nu_l$$

As for richness, we modeled the variance of within-group errors (ε_{jkl}) using a corAR1 correlation structure. In addition, we modeled the variance as an exponential function (varExp) [S15] due to the pattern of non-constant variance in a plot of the standardized residuals against fitted values for a model implementing a constant variance structure. This approach alleviated the heteroscedasticity of residuals and improved model fit.

Most published studies presented means of alpha biodiversity (S or H') at the site level or gamma biodiversity; thus our lowest unit of observation for these datasets was either mean alpha-S (or H') or gamma-S (or H') at each time point. Equations 1 and 3 modeled the effect of time on richness and diversity, respectively, at the site level, given study and sub-study factors whose effects were modeled in Equations 2a, 2b, 2c, 4a and 4b.

In addition to our hierarchical model that estimates trends across the full dataset, we conducted a post-hoc analysis to estimate roughly how many of the time-series might be considered significantly positive or negative. To assess significance, we added the 95% confidence interval for the random effect of year from the full mixed-effects model to the fitted slope for each time-series. Time-series trends were considered significant if the confidence intervals did not overlap with zero. We then calculated the percentage of significant time-series as a fraction of the total number of time series. This approach yielded 15.9% and 2.6% of richness time-series that were significantly positive and negative, respectively. For diversity, 5.9% and 3.0% of the time-series were significantly positive and negative, respectively.

In our analysis, study duration did not significantly influence temporal trends in richness (Table

S1, Figure 1). Nevertheless, about 2/3 of the richness data were compiled from time-series shorter than 15 years (3511 of 5073 observations; Figure 1), raising concern that the overall positive trend in richness over time was driven by short studies, many of which began after 2000. To address this point, we removed time-series shorter than 15 years and tested whether the effect of year remained positive and ecologically relevant. Although the effect was weaker, richness increased over time, and the inclusion of year still resulted in improvement over the null model ($\Delta i = 3.2$). Therefore, the conclusion that richness has increased over time in our dataset is robust to the removal of short studies.

We tested for publication bias in our dataset using funnel plots where sample size (i.e., precision) is plotted against effect size [S19]. In the absence of publication bias, this type of plot should reveal a funnel, with large variance in effect size at small sample sizes, and decreasing variance in effect size with increasing sample size. We used the number of temporal replicates as our estimate of precision, because the effect size of interest was the rate of change between S (or H') and time (i.e. slope). The richness and Shannon diversity datasets both revealed patterns consistent with a funnel (Figure S2). Importantly, there was no absence of time-series (points) with low effect sizes (i.e., slope ~ 0) and few temporal replicates. We conclude that our dataset of time-series is not biased towards those exhibiting statistical significance.

For visualization, we standardized the effect of year and study duration prior to model averaging to ensure that the scales of all six predictors were comparable [20]. Therefore, in the richness dataset year and study duration were rescaled so that their standard deviations were 0.5; in the diversity dataset these two predictors were rescaled so that their standard deviations were 1. We

did not similarly rescale the response variables (S or H'), or initial biodiversity (S or H'), because both were already rescaled through the use of a log transformation [S20]

All analyses were conducted in R 3.0.2 [S21] and the package ‘ggplot2’ [S22] was used for graphics. We used the package ‘nlme’ [S23] for mixed-effects modeling and ‘AICcmodavg’ [S24] for model selection and averaging.

Supplemental References

- S1. Frid, C.L.J., Garwood, P.R., and Robinson, L.A. (2009). Observing change in a North Sea benthic system: A 33 year time series. *J. Mar. Syst.* *77*, 227-236.
- S2. Gooday, A.J., Malzone, M.G., Bett, B.J., and Lamont, P.A. (2010). Decadal-scale changes in shallow-infaunal foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. *Deep-Sea Research 2* *57*, 1362-1382.
- S3. Gotelli, N.J., and Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* *4*, 379-391.
- S4. Barrett, N.S., Edgar, G.J., Buxton, C.D., and Haddon, M. (2007). Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. *J. Exp. Mar. Biol. Ecol.* *345*, 141-157.
- S5. Friedlander, A.M., and Parrish, J.D. (1998). Temporal dynamics of fish communities on an exposed shoreline in Hawaii. *Environ. Biol. Fishes* *53*, 1-18.
- S6. Beukema, J.J., and Dekker, R. (2011). Increasing species richness of the macrozoobenthic fauna on tidal flats of the Wadden Sea by local range expansion and invasion of exotic species. *Helgol. Mar. Res.* *65*, 155-164.
- S7. Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., and Magurran, A.E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* *344*, 296-299.
- S8. Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., et al. (2008). A global map of human impact on marine ecosystems. *Science* *319*, 948-952.

- S9. Whittaker, R.H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecology* 30, 279-338.
- S10. Tuomisto, H. (2010). A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* 164, 853-860.
- S11. Byrnes, J.E., Reynolds, P.L., and Stachowicz, J.J. (2007). Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 2, e295.
- S12. Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., DeFrenne, P., Verheyen, K., and Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci. USA* 110, 19456-19459.
- S13. Gelman, A., and Hill, J. (2006). Data Analysis Using Regression and Multilevel Hierarchical Models, (Cambridge University Press).
- S14. Bolker, B., Brooks, M., Clark, C., Geange, S., Poulsen, J., Stevens, M., and White, J. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24, 127-135.
- S15. Pinheiro, J.C., and Bates, D.M. (2000). Mixed-effects models in S and S-PLUS, (New York, NY: Springer).
- S16. Fisher, R.A., Corbet, A.S., and Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12, 42-58.
- S17. Magurran, A.E. (2004). Measuring biological diversity, (Oxford, UK: Blackwell Science).

- S18. Zuur, A., Ieno, E., Walker, N., Savaliev, A., and Smith, G. (2009). Mixed Effects Models and Extensions in Ecology with R, (Berlin: Springer).
- S19. Møller, A.P., and Jennions, M.D. (2001). Testing and adjusting for publication bias. *Trends Ecol Evol* 16, 580-586.
- S20. Gelman, A. (2008). Scaling regression inputs by two standard deviations. *Stat. Med.* 27, 2865-2873.
- S21. R Development Core Team (2013). R: A language and environment for statistical computing. (Vienna, Austria: R Foundation for Statistical Computing).
- S22. Wickham, H. (2009). ggplot2: elegant graphics for data analysis, (New York: Springer).
- S23. Pinheiro, J.C., Bates, D., Debroy, S., Sarkar, D., and R Core Team (2015). nlme: Linear and Nonlinear Mixed Effects Models. R Package version 3.1-120 Edition. (Vienna: R Foundation for Statistical Computing).
- S24. Mazerolle, M.J. (2013). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.32 Edition. (Vienna: R Foundation for Statistical Computing).