

University of Groningen

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

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

*Published in:*  
Current Biology

*DOI:*  
[10.1016/j.cub.2015.05.030](https://doi.org/10.1016/j.cub.2015.05.030)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2015

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Elahi, R., O'Connor, M. I., Byrnes, J. E. K., Dunic, J., Eriksson, B. K., Hensel, M. J. S., & Kearns, P. J. (2015). Recent Trends in Local-Scale Marine Biodiversity Reflect Community Structure and Human Impacts. *Current Biology*, 25(14), 1938-1943. <https://doi.org/10.1016/j.cub.2015.05.030>

### Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

### Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

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

Robin Elahi,<sup>1,2,\*</sup> Mary I. O'Connor,<sup>2</sup> Jarrett E.K. Byrnes,<sup>3</sup> Jillian Dunic,<sup>3</sup> Britas Klemens Eriksson,<sup>4</sup> Marc J.S. Hensel,<sup>3</sup> and Patrick J. Kearns<sup>3</sup>

<sup>1</sup>Hopkins Marine Station, Stanford University, Pacific Grove, CA 93940, USA

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

<sup>3</sup>Department of Biology, University of Massachusetts, Boston, MA 02125, USA

<sup>4</sup>Department 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](mailto: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

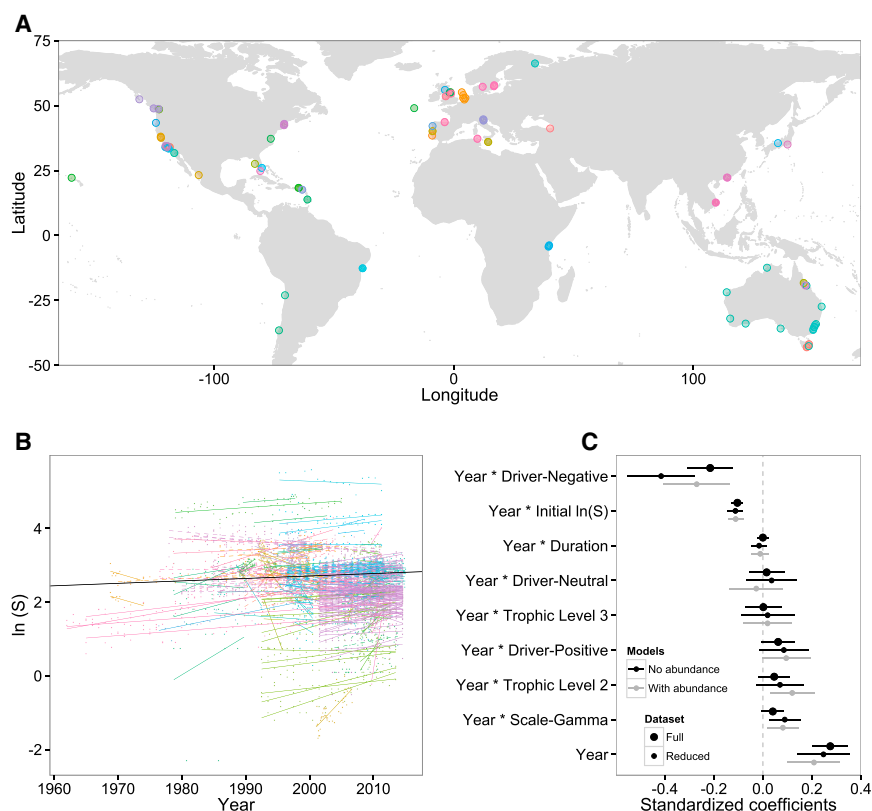
Near-shore marine environments harbor a wealth of biodiversity [12] and provide valuable ecosystem services to humans [13].

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

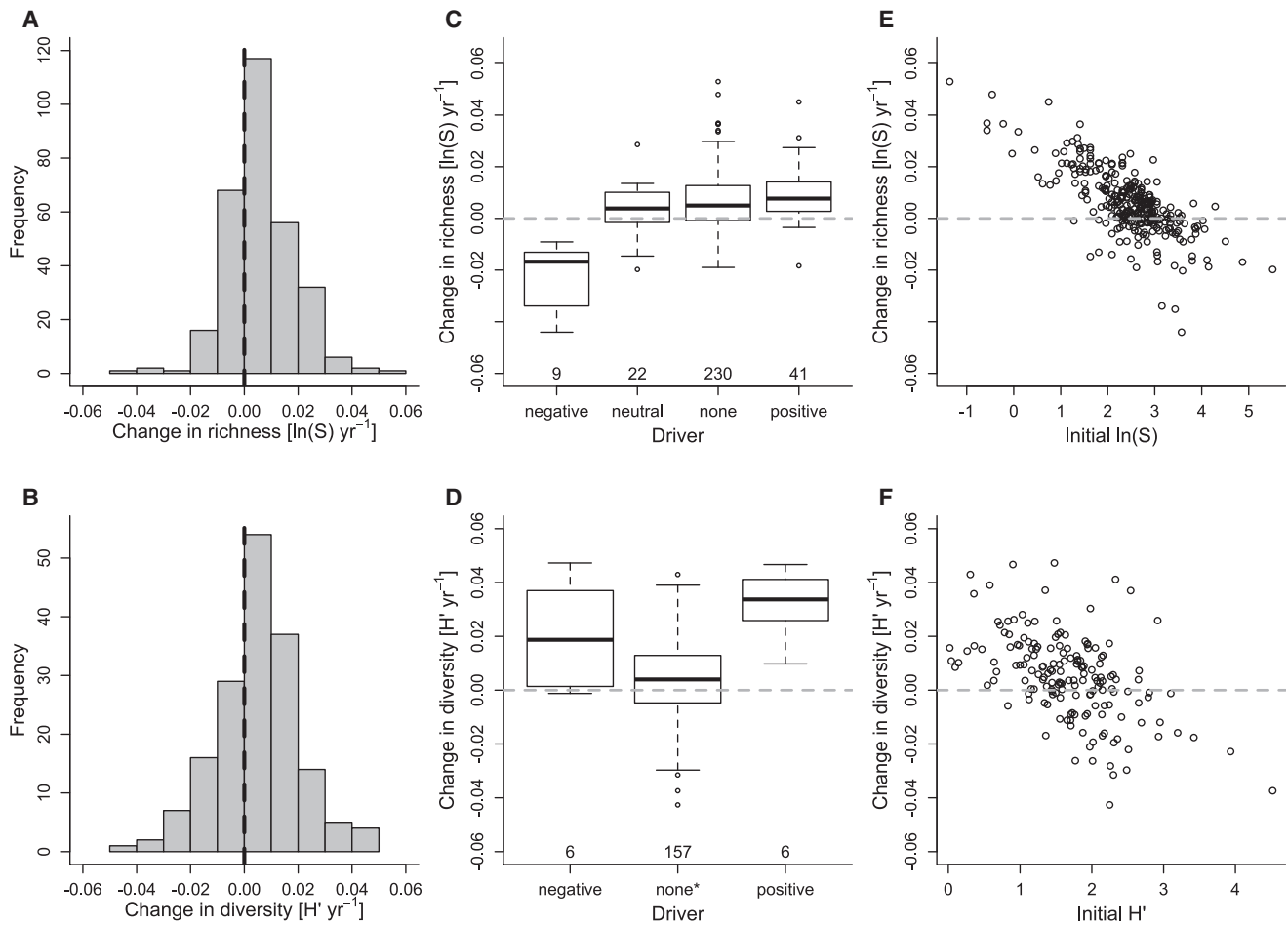
same set of candidate models as the full dataset (small black points) and the second with a set of candidate models that also included abundance as a predictor (see [Table S1](#)). The sizes of points representing full and reduced datasets are scaled relative to their number of observations. See also [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  $\times$  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  $\times$  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 ( $\Delta i$ ) 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  $\geq 0.9$ , 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.ternet.edu/vinp>; <http://sbc.ternet.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. Hamik, 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 Whitlatch, 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).