Human activities influence the direction and magnitude of local biodiversity change over time

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Abstract

In recent decades, environmental drivers of community change have been associated with changes in biodiversity from local to global scales. Here we evaluate the role of anthropogenic drivers in marine ecosystems as drivers of change in local species richness with a meta-analysis of a novel dataset of temporal change in species richness. We paired biodiversity data from 144 sites with large-scale drivers derived from geospatial databases: human cumulative impacts, sea surface temperature change, nutrient loading, and invasion potential. Three specific drivers (nutrient inputs, rate of linear temperature change, and non-native species invasion potential) explained patterns in local species richness change. We show that these drivers have opposing effects on biodiversity trends, and in some cases, contrasting directions of change can offset each other to yield observations of no net change across localities. Further, long-term studies reveal different effects of drivers that are not observed in short-term studies. These findings begin to explain high variability observed in species diversity trends at local scales. We suggest that local species diversity change is a predictable phenomenon and that observations of no net change across many time-series can be explained when the contrasting effects of human impacts are considered.

Keywords: global biodiversity change, human impacts, marine, coastal, attribution, meta-analysis

INTRODUCTION

Human impacts such as habitat destruction, pollution, and climate change have reduced global species diversity [1,2]. At the same time, local temporal trends in diversity are variable; synthetic assessments of marine and terrestrial diversity time-series have reported decreases, gains [3,4], and no net change in average species richness [5,6] over time at local scales (e.g., < 20 km^2). Even more important than variation in average trends reported by each of these syntheses is the ‘within-synthesis’ variation in local biodiversity trends. That is, individual sites can exhibit species losses or gains [3,5,6]. Emphasis on global average trends in diversity obscures the regional or local scale processes that drive local change in richness [3].

Human-mediated disturbances contribute to local species loss across terrestrial [2,7], aquatic [8], and marine environments [9,10]. However, to date, we lack studies that attribute local richness change over time to human drivers, instead using space-for-time substitutions (e.g., 2,7). Habitat change, overexploitation, and pollution negatively affect species at a local scale [11–14]. Meanwhile, synergisms between multiple stressors can exacerbate community responses to human impacts [15,16]. However human impacts such as invasions and climate change can lead to local increases in diversity [17,18]. If multiple drivers interact or co-occur, the opposing effects of these different drivers of global change could result in observations of no net change. Given the broad range of human impacts and the variability of community responses, it is not surprising that the findings of recent syntheses of local diversity change have been equivocal, especially since few of them have considered this variability in the context of human impacts [3].

High variability in diversity trends across many time-series underlies recent estimates of no average change in species richness. For example, the rates of species richness change in Vellend [5], which concluded no net change in species richness, ranged from losses of 8% per year to gains of 35% per year. Elahi [3], found more increases in richness over time than decreases, based on reported species losses that ranged from 5% per year to gains of 6.3% per year, and much of this variation was attributable to human drivers. This variability in observed patterns of diversity change and knowledge that human impacts affect local-scale diversity [2,3,7] suggests a need for a framework that explicitly identifies how environmental and human impacts will shape long-term changes in local-scale biodiversity. Here we attempt to attribute local changes in species richness to human impacts for a new synthesis of species diversity over time in marine coastal communities.

Coastal communities worldwide are subjected to a range of different human impacts [19]. We hypothesize that cumulative human impacts are likely to reflect additive stresses and thus have a negative effect on local species richness [16]. However, cumulative impacts are composed of many individual drivers that could mask each other’s signal. We quantify how a combination of the human impacts—nutrient addition, shipping traffic, and rate of temperature change—affect species richness change in marine communities at a local/site level. Nutrient addition can negatively affect local richness by degrading habitat [20,21] but can also increase productivity, and consequently total abundance and therefore diversity. Shipping traffic facilitates species invasions and can lead to gains or offset local losses by introducing new species [22]. Increased temperatures could lead to species range expansions yielding local gains of warm water species [23–25]. Last, we expect the effect of drivers on diversity can change over time [26]. Thus, we examined how study duration to moderates the effect of drivers. To address these hypotheses, we collated studies that have measured species richness from sites across marine biomes and leverage the available variation in global drivers to put our analysis in an ecological context. We find that variation in local-scale biodiversity change is related to the influence of human impacts such as climate change, invasions, and eutrophication.

METHODS

Study Selection

We performed a systematic search of the literature using Web of Science and the Aquatic Commons database, which included grey literature publications. Additional grey literature publications were extracted from Elahi [3], which was published after our initial search. We searched for studies that had resampled marine species richness or diversity at a minimum of two time points equal to or greater than one year apart. Our literature search terms were adapted from Vellend [5] with keywords to target marine habitats while excluding freshwater or terrestrial habitats: e.g., 'marine' OR 'ocean' NOT ('freshwater' OR 'terrestrial'), and combining these with keywords about biodiversity and resampling: ('biodiv* OR 'divers*' OR 'richness') AND 'resamp*' (See full search string in supplementary materials S1). We initially entered the search terms into the Web of Science and Aquatic Commons databases on February 19, 2014. This search returned 4803 references, which we filtered down to 745 papers after reviewing titles, abstracts, and full text where necessary, to identify studies that met the following criteria: sampled marine taxa, reported biodiversity, and resampled sites with at least one year between initial and final sampling points (figure S1). From the remaining 745 papers, we excluded studies if sampling methods were inconsistent between time points, if rare species were not included, or if *a priori* events were described by authors as affecting a site (see supplementary materials S2).

After study selection we had data from 144 sites from 35 studies around the world (figure S2). Although we collected data for abundances (sites = 22) and Shannon diversity (sites = 40), the number of samples and the limited range of variation in drivers were insufficient for us to examine in the context of human drivers. Therefore, we discuss only results of local species richness change.

Data Acquisition

We extracted 13 variables that described taxonomic group, sampling method, number of replicates, number of subsamples, plot size, and richness. In most studies, raw species abundance data were not provided and so data were extracted as summary statistics from figures using WebPlotDigitizer 3.10 [27] or manually extracted from data tables. Wherever possible, sampling errors from summary statistics were collected so that we could perform a variance-weighted meta-regression. When a site was sampled between a range of years (e.g., 1995 – 1996), the first year was recorded for consistency. When only a season or range of months was given, the average month of that season was recorded. When studies explicitly stated that an event had occurred (e.g., Marine Protected Area implemented, resource extraction, construction) they were excluded from the analysis. We calculated the effect size as the log response ratio (LRR) of the proportion of species richness change between a final and initial time point (eqn. 1).

LRR = Ln(Final richness / Initial richness) (eqn. 1)

We chose to use the LRR instead of Hedges's D, another commonly used metric of effect size, because log transformation of the response ratio normalizes the data and because we can use the following equation to convert the LRR into the percent change in species richness (eqn. 2).

% change in species richness = $100 * (e^{\mathrm{LRR}} – 1)$ (eqn. 2)

We verified assumptions of normality of residuals for all fit models using visual inspection of standardized residuals and their quantiles. To check for potential publication bias in effect sizes, we visually inspected funnel plots. However, publication bias in our dataset was unlikely as many of our studies (46%) were not testing for changes in biodiversity over time. For a complete list of studies used in the analysis see electronic supplementary materials S5.

Driver data

To examine the effect of human impacts on the change in species richness over time, we used components of the cumulative human impacts (CHI) data created by Halpern [28]. The CHI model summarizes data on a broad set of human impacts for every square kilometer of the world's oceans. Impact scores are derived from a model that integrates global data for 19 different drivers including nutrient pollution, fishing, urban runoff, shipping traffic, and sea surface temperature anomalies [28]. The CHI model is a potential indicator of human impacts; however, this model incorporates the effects of multiple drivers that may have opposing effects on local species diversity. To understand the effects of specific drivers on local-scale species richness change, we extracted data layers that had global coverage and that were expected to affect local richness in coastal areas. We used two data layers used in the CHI data: non-native species invasion potential (metric tonnes of cargo shipped to a port in 2011 was used as a proxy for invasion potential) and nutrient addition (metric tonnes of nitrogen and phosphorous fertilizer use as reported by the FAO from 2007 – 2010, was used as an indication of intensity of nutrient addition along coastal areas; See [19,28] for details). We also calculated the decadal rate of linear temperature change (LTC) using the Met Office Hadley Centre Sea Surface Temperature data [29]. For each study, we collected the latitude and longitude of sampling points for all plots surveyed in a study. When study sites were composed of multiple subsamples, we included all the associated coordinates. Data from the spatial layers were then extracted from these coordinates. When a site was comprised of multiple coordinates, we computed the average impact value for each site.

Statistical analysis

To examine whether marine richness has changed at local scales and to test whether cumulative human impacts and specific drivers affect changes in local species richness, we performed three variance-weighted random effects meta-regressions using the package *metafor* [30] in the statistical software R version 3.4.0 [31]. We included a random effect of study, as single studies could contain multiple sites. This approach allowed us to account for variation between studies due to factors such as differences in researcher methods, taxonomic groups, and sites. All code for analysis is available at https://github.com/jdunic/local-marine-meta.

To test explicit drivers and to determine the average rate of change in local species richness we tested three models: the average change in local richness (eqn. 3), the effect of cumulative human impacts on local richness change (eqn. 4), and the effect of specific drivers on local richness change (eqn. 4). We used the model heterogeneity statistic Q_m to determine whether our models explained a significant amount of variability observed in the data. We first examined the average rate of change in species richness from our data set using the following model for site *i* from study *j*

$$LRR_{ij} = \alpha_j + \beta_D Duration_i + e_i$$

$$\alpha_j \sim N(0, \sigma_j)$$

$$e_i \sim N(0, \sigma_i)$$

(eqn. 3)

Where αj is the between-study random effects (estimated by the model) and σ_i was the measured variance of a richness estimate at site *i*. We used study duration as a predictor of the LRR to estimate a rate of change rather than use LRR/Duration as a response variable to increase the power of our analyses. To then evaluate the effects of different drivers, we used a general model for incorporating k drivers (eqn. 4).

$$\mathrm{LRR_{ij}} = \alpha_\mathrm{j} + \beta_\mathrm{D}\mathrm{Duration_{ij}} + \sum_{k=1}^{n}(\beta_\mathrm{k}\mathrm{Driver_{ijk}}) + \sum_{k=1}^{n}\left(\beta_\mathrm{k2}\mathrm{Driver_{ijk}Duration_{ij}}\right) + \mathrm{e_i}$$

$$\alpha_\mathrm{j} \sim \mathrm{N}(0, \sigma_\mathrm{j})$$

$$\mathrm{e_i} \sim \mathrm{N}(0, \sigma_\mathrm{i})$$

(eqn. 4)

Including duration in our analysis allowed us to account for differences observed between short-term and long-term studies by comparing the rate of change of richness as it varies by study duration (β_D) with the average effect of a driver on the rate of change of species richness (β_k) and the average effect of a driver on the rate of change of richness as moderated by study duration (β_{k2}). For example, a positive value for the coefficient β_{k2}, would be interpreted as the driver slowing the rate of loss or increasing the rate of gain, depending on the sign of rate of change β_D. We used the Akaike Information Criterion corrected for small sample sizes (AICc) to compare models and determine whether inclusion of human impacts improved the predictive ability of the model relative to the model that included only study duration.

To determine whether any single study had a disproportionate effect on parameter estimates we systematically re-ran the meta-analysis excluding data from one study at a time to test the robustness of our analyses to outliers in the data (i.e., leave-one-out analyses). We used variance weighting in our analysis because it increases the power to detect differences from zero by placing higher values on studies for which estimates are more precise [32]. Although using an unweighted or sample-size weighted analysis would increase the studies included in our analyses, the parameter estimates from these methods are unreliable (figure S4). For completeness, however, we present these results along with their robustness to the exclusion of single studies using both method (supplementary materials S3, S4, figures S5-S9, tables S5 – S8).

Taxonomic groups

We expect that there will be differences in rates of richness change across taxonomic groups in response to different stressors [7,33]. Therefore, in addition to testing the effect of global drivers of change on local richness change, we subset the data by taxonomic group. For each taxonomic group we had insufficient sample size to test the effect of multiple global drivers on local richness change. Therefore, we present only results for the mean rate local richness change without considering human impacts and the effect of cumulative human impact values on the rate of local richness change for different taxonomic groups.

RESULTS

Local richness change

In general, inferences on the rate of change of species richness depend on the inclusion of human impacts. Within our dataset, both models that included some form of human impacts performed better than the model that did not include human impacts (table 1). In our model that did not consider human impacts, study duration influenced observed change in species richness (Q_m = 5.12, p = 0.024) and we found that the average log rate of change in species richness per year was 0.01 (95% CI = 0.002 - 0.021, p = 0.022), which corresponds to species richness gains at a rate of 1.05% per year (figure 1*a*, table S1). When we included cumulative human impacts and specific drivers in our models, the mean estimated log rate of change in species richness changed over study duration. For example, when cumulative human impacts were zero (i.e., the duration effect in Fig. 1b), the observed rate of change in species richness was -3.2% (95% CI = -5.4% – (-1.1)%, p = 0.004, table S1) per year and when all specific driver values were zero (i.e., the duration effect in figure 2), the observed rate of change in species richness was 1.7% (95% CI = 0.19% – 3.3%, p = 0.027, table S1) per year.

Cumulative human impacts accounted for a significant proportion of the heterogeneity observed in our dataset (Q_m = 45.3, $p < 0.001$), but the signs of results were unexpected. There was weak evidence for negative effects of cumulative human impact values on the species richness from short-term studies (i.e., the CHI effect in figure 1*b*), with an associated decline in species richness of -4.6% per unit of cumulative human impact value (95% CI = -9.6% - 0.6%, p = 0.081; table S1). However, over the long term (impact * duration interaction in figure 1*b*), each unit increase in cumulative impact value decreased the rate of species loss per year by 0.86% / (year * impact score) (95% CI = 0.5% - 1.3%, p = < 0.001; table S1).

Different drivers had opposing effects on local richness change when we accounted for nutrient addition, invasion potential, and rate of linear temperature change in our models (Q_m = 60.3, $p < 0.001$, figure 2, 3, table S1). Nutrient addition alone was associated with increases in local gains of richness at a rate of 1.3% per tonne of nutrients / km^2 (95% CI = 0.4% - 2.2%, p = 0.007, table S1). Similarly, rate of linear temperature change was also associated with gains (6% increase per ˚C / decade, 95% CI = 1% – 11%, p = 0.018, table S1). Conversely, there was weak evidence for negative effects of invasion potential (-1.4% per 1000 tonnes of shipping cargo, 95% CI = 0.4% - 2.3%, p = 0.066, table S1). However, when we considered the effect of these drivers over time ($\beta_{Duration*Driver}$), the effect of each driver on local richness was reversed (i.e., the Duration:Driver effect in figure 2*b*). Nutrient addition and rate of linear temperature change negatively affected the rate of species richness change over time, while invasive propagule pressure positively affected the rate of species richness change over time (table S1). Figure 3 illustrates the expected effects of nutrients, invasive propagule pressure, and rate of linear temperature change (when set to the maximum values observed in our data) on the rate of species richness change over time compared to a baseline rate of change (1.7% per year) when the three driver values are zero. The observed net effect of richness change, when all drivers were set to the maximum values observed in our dataset (figure 3*d*), shows a much smaller effect size over time compared to any individual driver. This suggests that opposing effects of local drivers can result in observations of little to no change in global averages of local richness change.

Taxonomic groups

Responses to changes in local richness may vary depending on the subset of the community examined. Our dataset included nine different taxonomic groups, five of which had three or more sites sampled (table S2). When impacts were not considered, we found gains in local richness at an average rate of 5.5% per year in algal assemblages and gains at a rate of 8.1% per year in invertebrate assemblages (figure 4) in the context of our dataset. Like the aggregated dataset, the inclusion of cumulative human impacts (table S3) generally improved model performance (table S4) when we considered taxonomic groups separately. Unfortunately, sample sizes were insufficient to test for the effects of drivers on local richness change across taxonomic groups.

Data coverage

With respect to global representativeness of impact levels, we had more observations of species richness change over time than expected in intermediate levels of nutrient addition and invasion potential compared to the distribution of these two drivers when considered from coastal areas globally (figure S10*a*,*b*). Meanwhile, the cumulative human impact values ranged from 0.89 – 8.9 in our analysis, compared to minimum and maximum global values of 0 to values greater than 15. Similar to the specific drivers, the majority of our sites showed moderate impact. Fifty percent of our studies were in regions/pixels with cumulative human impact values between 2.7 and 5.1. Across taxonomic groups our data were limited to algae, fish, and invertebrate communities, or some combination of these taxonomic groups (mixed). Meanwhile, temporally, eighty percent of studies were 15 years or less in duration and started after 1990.

DISCUSSION

Our meta-analysis suggests that local context of human impacts is necessary to understand the high variability observed in long-term change in local species richness. Specifically, local drivers (nutrients, invasion potential, and the rate of linear temperature change) can have opposing effects on local changes in species richness. These opposing effects can interact such that the net change in local species richness can be close to zero when multiple drivers are acting on a community, as illustrated in figure 5*d*. As expected, when we considered cumulative human impacts, we found weak evidence for negative effects on local richness change. But over time, contrary to expectations, we found that cumulative human impacts were correlated with local gains in richness. This was unexpected given research showing that cumulative stressors typically have a negative effect on local communities [16,34]. However, the cumulative human impacts are an aggregate metric of human impact meaning that observed relationships between local scale richness change and high impacts may be driven by whatever individual driver is most important at a given location. Our results, which indicate differences in the direction of change in local species richness change due to specific drivers, suggest a need to apply ecological theory about individual drivers of species richness at a local scale to the entire planet to generate *a priori* predictions of when and where we should observe increases or decreases in biodiversity.

Nutrients

We found that, while sites associated with high nutrient run-off were associated with short-term gains in species richness, over the long-term, sites with high nutrient run-off were correlated with losses (figures 2, 3). Nutrient addition has been shown to increase primary production [35] and richness [36] in macroalgae and may be, in part, responsible for the increase in algal richness that we observed (figure 4). However, the processes that drive effects of nutrient addition on local communities can be complex and depend on factors such as the level of addition [37], species interactions [38], and dependent on time [39]. Most nutrient addition studies in marine systems occur over a short time frame (e.g., 40,44,45), but Kraufvelin [39] found that it could take five years before significant changes in canopy composition of rocky shore macroalgae are observed. Meanwhile in terrestrial systems, long-term studies in grasslands have also revealed that nitrogen addition can result in species losses over time [42]. Our results suggest that nutrient addition is an important driver of local richness change and that in the long-term nutrient enrichment can decrease rates of local richness change. Given the dynamics of coastal systems, this might even be more important in estuarine systems where water exchange is low relative to the open coast.

Invasions

We found that in the short-term, there was weak evidence that invasion potential may be associated with species richness losses, but in the long-term, high invasion potential was associated with local gains in species richness. Invasions can augment local species gains if new-invaders can facilitate potential future invaders [43] through mechanisms such as habitat change

[33,44]. Our finding that long-term gains in species richness are associated with high shipping traffic is consistent with predictions made by Drake [45] and Sax [46]. Elahi [3] also found an average increase in local species richness in coastal marine communities over time, particularly for low trophic levels. When we considered separate taxonomic groups we found substantial increases in both the invertebrate and algal communities, which is consistent with the type of invaders that are transported by shipping traffic through ballast waters and organisms attached to ship hulls [44]. Furthermore, our findings of increased richness of lower trophic levels are consistent with expectations of long-term gains in richness of primary consumers in marine systems[47]. This suggests that more detailed context, such as taxonomic group or trophic level, could be necessary to understand patterns of local richness change and the effect of propagule pressure on local richness change.

Temperature

Similar to the effects of nutrients on local richness, negative or low values of rate of linear temperature change were associated with short-term gains but increases in the rate of temperature change were associated with local species losses (figure 2). Further this result did not appear to be strongly influenced by any one study. Our observation of short-term gains and long-term losses might reflect situations where warm water species move into areas that were previously at cooler temperatures at a rate that is faster than the emigration or extinction of resident species [48,49]. For example, within the studies included in our analysis, the movement of warm water fishes into areas that had previously cooler water temperatures was found in two of eleven studies examining fish communities (e.g., 53,54). Therefore, it is important to consider long-term trends in species richness as gains due to species range expansions or species introductions could offset local losses. In a meta-analysis to examine the effects of human impacts on local species richness, Murphy [7] found that increased temperature was not a significant moderator of richness in producer and ectotherm communities yet the majority of studies included in Murphy [7] were less than three years in duration.

Relationship to the ongoing debate on trends in local species diversity

Broadly, our results urge caution in the interpretation of the literature on average trends in local scale biodiversity without considering local context. First, as with previous syntheses, we identified additional geographical biases in our dataset similar to those identified in terrestrial systems and in other recent syntheses of local diversity change [2,3,5,6]. Specifically, South America, Africa, Asia, and Antarctica were underrepresented. Biases of sampled sites may limit the ability to extrapolate the trends observed in our synthesis to the global scale if our dataset contains a non-representative distribution of impacts relative to all marine coastal diversity on the planet. The prevalence of drivers in our dataset differed from their global representation (figure S10). If the same is true of other recent analyses (e.g., [3,5,6]), the inference of average trends in species richness could reflect spatial biases in the distribution of drivers in the datasets of these studies rather than a true global average. Recent syntheses of hundreds of space-for-time analyses report that land-use change, invasive species, nutrient addition, and habitat change are associated with declines in local-scale species richness [2,7]. When these results are translated to global maps of impacts, they suggest that richness change in terrestrial systems should be negative, on average [2]. Our results begin to attribute the magnitude and sign of local-scale species richness change to specific human impacts. Further, our results show that specific human drivers can have antagonistic effects on local richness change. We suggest a need to develop an understanding of the current and future distribution of drivers, including ones not explicitly considered in this study, to understand local species richness change across the world's oceans. We conclude that examinations of change in biodiversity that come from non-representative samples must either take drivers into account or restrict inferences to the biogeographic regions considered. This point is essential whether an analysis focuses on either temporal analysis or space-for-time substitutions.

CONCLUSION

How global increases in species extinction rates are being manifest at local scales is of immense concern to basic and applied ecological research. Our analysis shows that local context of human drivers explains some of the high variability observed in trends in local species richness. Knowledge of specific drivers of local richness change such as invasion potential, nutrient addition, and temperature change help predict changes in local scale richness. Our results combined with others [2,3,7] suggest that to discern meaningful patterns of biodiversity change, we must have some knowledge of local context (e.g., recent disturbances, geographic position and context of human impacts, focal taxonomic group). We provide further context to the recent results that have suggested no net change in species richness at local scales, showing that multiple human impacts can contrast with each other with respect to species richness. We suggest that species richness change at local scales in coastal marine environments is an understandable and predictable phenomenon. To truly understand the future of local biodiversity in the world's oceans, we suggest combining decades of hard-won understanding of community ecology with new global assessments of human impacts across our seas. With these tangible, testable predictions in hand, we can begin to plan for the oceans of the anthropocene.

Data accessibility

Data will be stored in the Knowledge Network for Biocomplexity (KNB) repository. Associated R scripts will be archived with the data as well as via github and referenced using a Zenodo DOI.

Competing interests

We have no competing interests

Author contributions

JD and JB conceived of the study and study design. All authors contributed to data collection. JD managed the database and carried out the statistical analysis. JD and JB wrote the initial draft of the manuscript. All authors revised the manuscript.

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Tables

Table 1. AICc scores (corrected for small sample sizes) calculated for three variance-weighted meta-regressions of the log ratio of the proportion of species richness change (LR). The model which included three specific drivers: invasion potential (Inv), nutrient addition (Nut), and rate of linear temperature change (LTC) and the model that included cumulative human impacts (CHI) both performed better than the model that did not include any form of human impacts.

Model	Log-Likelihood	K	Deviance	AICc	∆AICc	Akaike weight
LR ~ Dur * (Inv + Nut + LTC)	-2492.09	7	5202.81	5004.06	0.00	1.00
LR ~ Dur + CHI + Dur*CHI	-2497.02	3	5212.67	5004.64	0.58	0.85
LR ~ Dur	-2518.69	1	5256.00	5043.61	39.55	0.00

Figures

Figure 1. (*a*) With increasing study duration, variance-weighted meta-regression shows that the log ratio of species richness at a rate equivalent to species richness gains of 1% per year. Studies, represented by different colours, could contain data from multiple sites and so studies were modelled as random effects. (*b*) Coefficient estimates for the relationship of the log-proportion of change in species richness as a function of study duration (Duration), short-term cumulative human impacts (CHI; Halpern [28]), and long-term effects of cumulative human impacts (Duration*CHI). Points represent coefficient estimates and lines represent 95% CI obtained using a variance-weighted meta-regression.'

Figure 2. The standardised coefficient estimates of the effect of three global drivers: nutrient addition (Nutrients), invasion potential (Invasives), and the decadal rate of linear rate of temperature change (LTC) on (*a*) the log-proportion of change in species richness in the short-term and (*b*) the effect of these drivers on the rate of change in the log-proportion of change in species richness over time. Points represent standardised coefficient estimates and lines represent 95% CI obtained using a variance-weighted meta-regression.

Figure 3. The predicted change in the log-proportion of change in species richness over study durations up to 20 years as moderated by each of the three drivers (*a*) nutrient addition, (*b*) invasion potential, (*c*) rate of linear temperature change when each is set to the maximum value observed in our dataset and the others are set to zero. The final plot (*d*) demonstrates the overall effect on the log ratio of local richness change when all three drivers are the maximum values observed in our dataset. Effects of drivers on predicted richness change (blue) are compared to the predicted change when all drivers are set to zero (grey). Predicted values regression lines and confidence intervals were obtained using a variance-weighted meta-regression from the full drivers model: LRR ~ Duration * (nutrient addition + invasion potential + linear rate of temperature change).

Figure 4. Coefficient estimates of the log-proportion of change in species richness in the five most sampled taxonomic groups (*k*, sites; *n*, studies) for the model containing study duration only. Points represent coefficient estimates and lines represent 95% confidence intervals using variance-weighted meta-regressions.

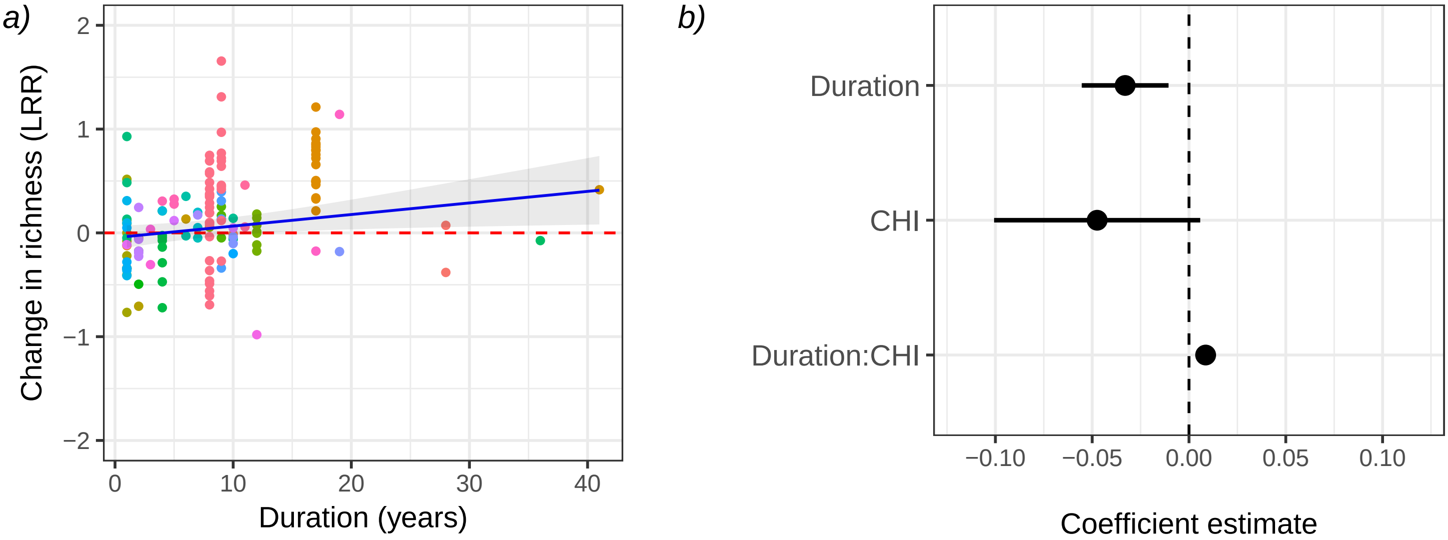
a)
b)
Change in richness (LRR)
2
1
0
−1
−2
0
10
20
30
40
Duration (years)
Duration
CHI
Duration:CHI
−0.10
−0.05
0.00
0.05
0.10
Coefficient estimate

Figure 1

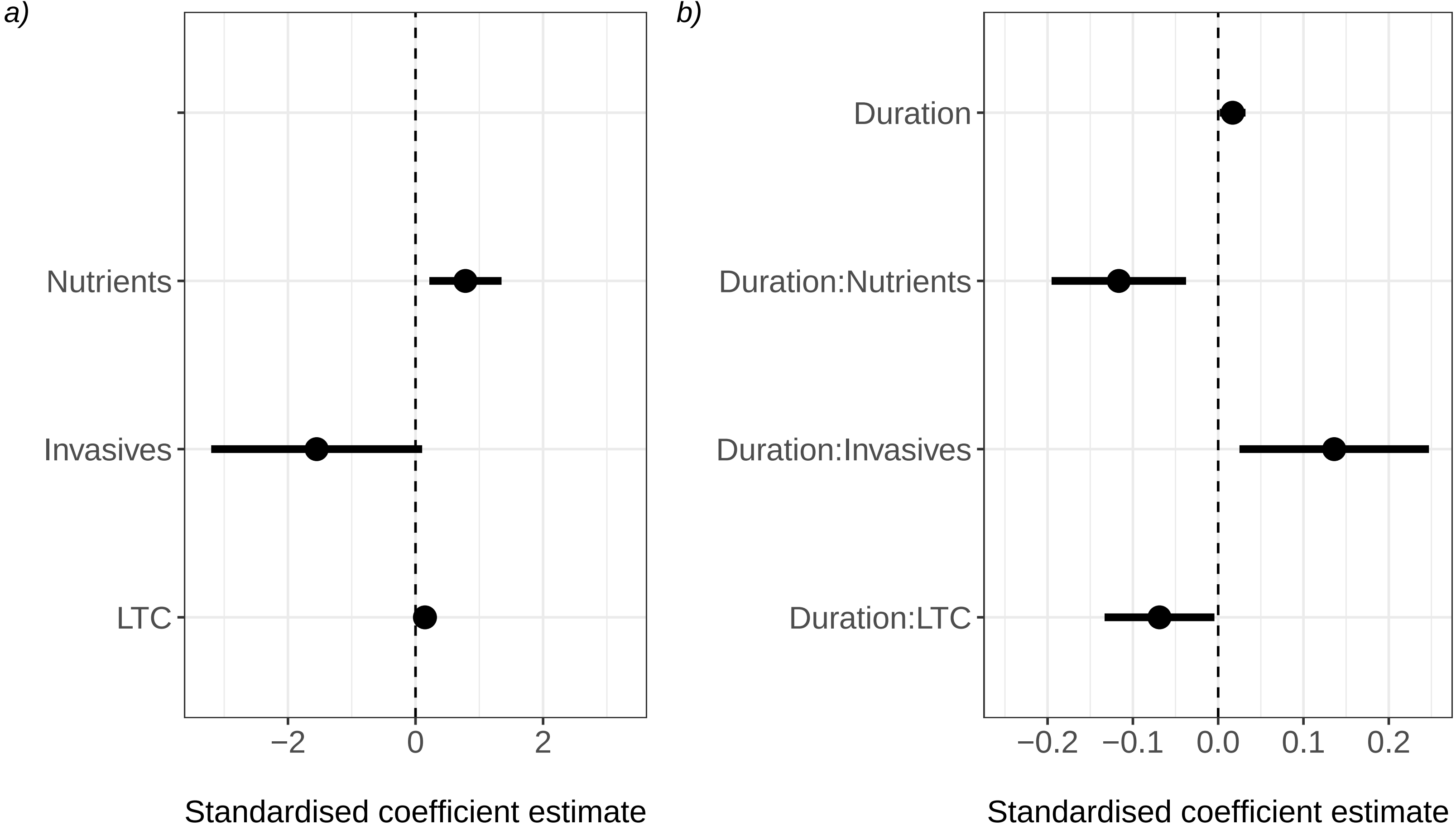
a)
Nutrients
Invasives
LTC
−2
0
2
Standardised coefficient estimate
b)
Duration
Duration:Nutrients
Duration:Invasives
Duration:LTC
−0.2
−0.1
0.0
0.1
0.2
Standardised coefficient estimate

Figure 2

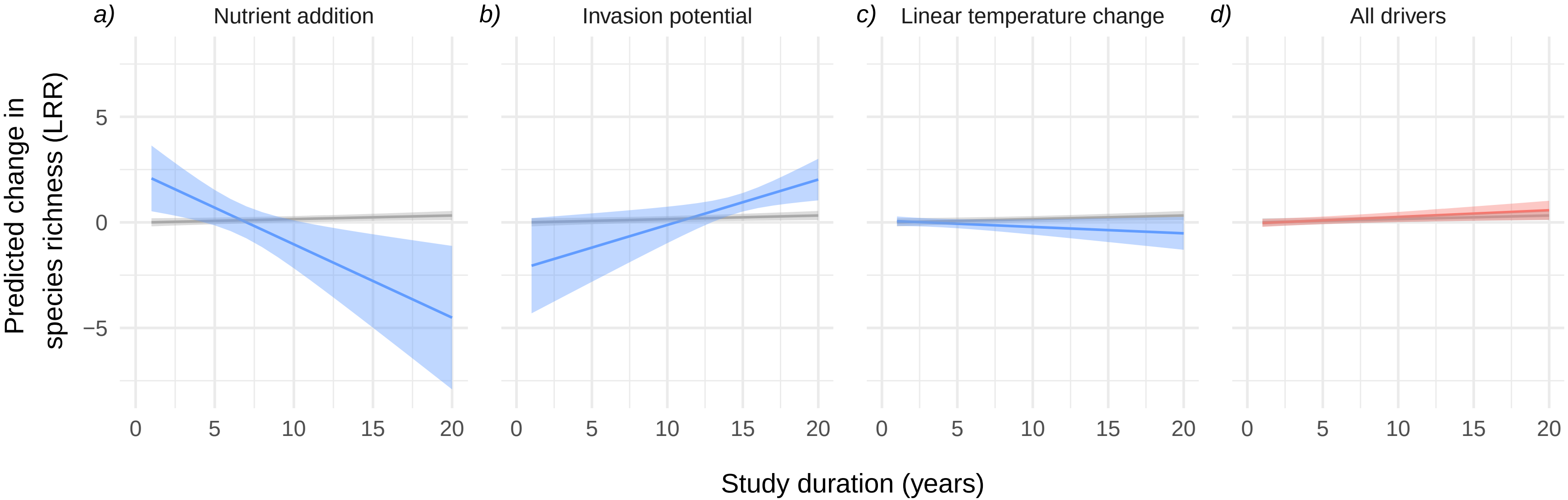
a)
Nutrient addition
b)
Invasion potential
c)
Linear temperature change
d)
All drivers
Predicted change in species richness (LRR)
5
0
−5
0
5
10
15
20
Study duration (years)

Figure 3

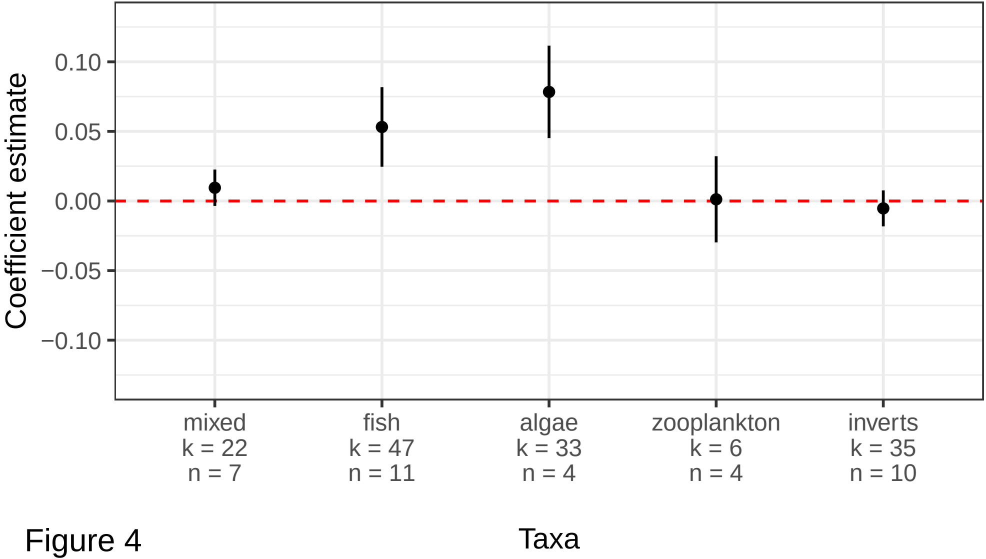
Coefficient estimate
0.10
0.05
0.00
−0.05
−0.10
mixed
k = 22
n = 7
fish
k = 47
n = 11
algae
k = 33
n = 4
zooplankton
k = 6
n = 4
inverts
k = 35
n = 10
Taxa

Figure 4