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# Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields

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Temperature variation within a year can impact biological processes driving population abundances. The implications for the ecosystem services these populations provide, including food production from marine fisheries, are poorly understood. Whether and how temperature variability impacts fishery yields may depend on the number of harvested species and differences in their responses to varying temperatures. Drawing from previous theoretical and empirical studies, we predict that greater temperature variability within years will reduce yields, but harvesting a larger number of species, especially a more functionally diverse set, will decrease this impact. Using a global marine fisheries dataset, we find that within-year temperature variability reduces yields, but current levels of functional diversity (FD) of targeted species, measured using traits related to species' responses to temperature, largely offset this effect. Globally, high FD of catch could avoid annual losses in yield of 6.8% relative to projections if FD were degraded to the lowest level observed in the data. By contrast, species richness in the catch and in the ecosystem did not provide a similar mitigating effect. This work provides novel empirical evidence that short-term temperature variability can negatively impact the provisioning of ecosystem services, but that FD can buffer these negative impacts.

## 1. Introduction

Temperature can substantially affect populations and their dynamics. As a result, considerable attention has focused on the impacts of projected changes in mean temperatures [1,2]. However, temperature variation within a year is often far larger than the predicted increases in mean temperature, even over multiple decades [3,4]. Small changes in temperature can have disproportionately large effects on biological processes, including growth, development and survival, because of their nonlinear relationship with environmental temperature [2,5–7]. Therefore, changing the variability around the mean temperature can dramatically alter rates of critical processes that affect population dynamics, abundance and species' distributions [7–11]. Furthermore, short-term fluctuations and temperature shocks can impact growth, abundance, phenology, behaviour and survival over timescales where species cannot adapt, adjust behaviour or move to a refuge [3,12,13]. Therefore, shifts in the magnitude and pattern of short-term temperature variation may have as large or larger population effects as long-term warming [4,14].

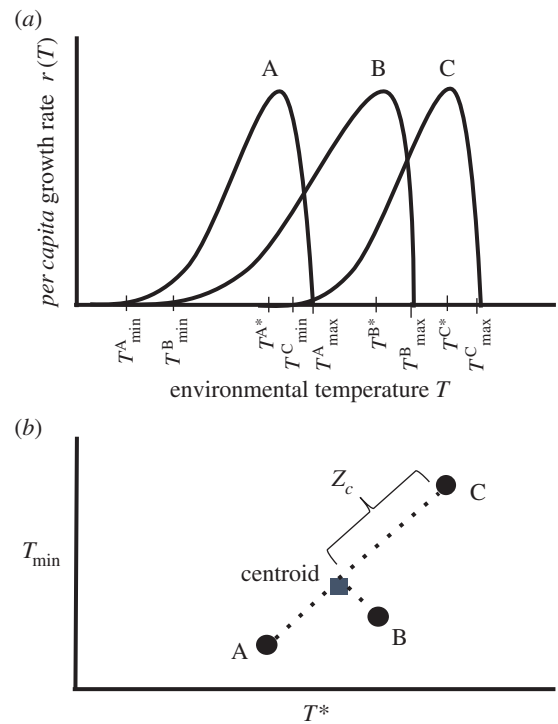
An important but underexplored question is whether the effect of within-year temperature variation on populations has consequences for ecosystem services, such as food provision from harvesting species. However, the impacts on yields could depend on the mix of species being harvested, because

individual species can respond differently to within-year temperature variation. Ecological research and theory suggest that species diversity can raise levels of ecosystem functions (e.g. productivity) in variable environments. For instance, when species compete for resources, differences in their responses to environmental fluctuations can lead to higher aggregate biomass than any single species could produce [15–17]. Furthermore, communities with more species may be more likely to contain productive or thermally tolerant species [18]. Most literature on how biodiversity interacts with environmental variability to influence ecosystem service provisioning focuses on inter-annual timescales [15,17]. However, the ability for biodiversity to buffer ecosystem services from short-term variability could have far-reaching implications. For instance, explicitly considering within-year variability, one theoretical study predicts that high phenotypic diversity within a functional group will result in higher long-term productivity than from any single species [19]. Similarly, diversity of thermal tolerance characteristics among harvested species could impact yields in the face of temperature variability, as sets of species with diverse temperature characteristics may be more likely to contain thermally tolerant species or species with opposing thermal responses.

Here, we empirically examine the relationships among short-term temperature variability, biodiversity and service provision from population harvest, using marine fishery yields as an example. Globally, marine fisheries provide employment, billions of dollars in income and over 79 million tonnes of protein annually [20]. Most previous studies focus on long-term trends (warming) or multi-year and decadal oscillations (e.g. ENSO), finding that variation in sea surface temperature (SST) across years significantly impacts fisheries yields [12,20–23]. The effects of short-term temperature variability on fisheries yields, however, have been considerably less studied despite many fish species being sensitive to shorter-term fluctuations [21,24]. Indeed, a recent study [25] found that within-year climatic variation correlates more strongly with fisheries population collapse than decadal and inter-annual temperature variation.

Several potential mechanisms could cause temperature variability within a year to affect fishery yields, including changes to adult growth, survival, phenology and fishing activity. First, short-term temperature variation affects individual growth and adult survival with consequences for adult harvestable biomass in that year and for population size over time (e.g. [26]). A species' physiological performance, such as *per capita* growth rates, depends nonlinearly on environmental temperature [5,6,27], including for fish [5,28]. For species adapted to the mean temperature in an ecosystem, this nonlinear relationship suggests that increased variation in temperature should reduce average performance [9,11,29], including by affecting adult biomass growth or other demographic parameters (e.g. survival rates). Empirical research finds support for these predictions [9,11,26] and shows that nonlinear effects of short-term temperature variation on *per capita* performance can have lasting population-level impacts on both ectotherms [10] and longer-lived endotherms [26].

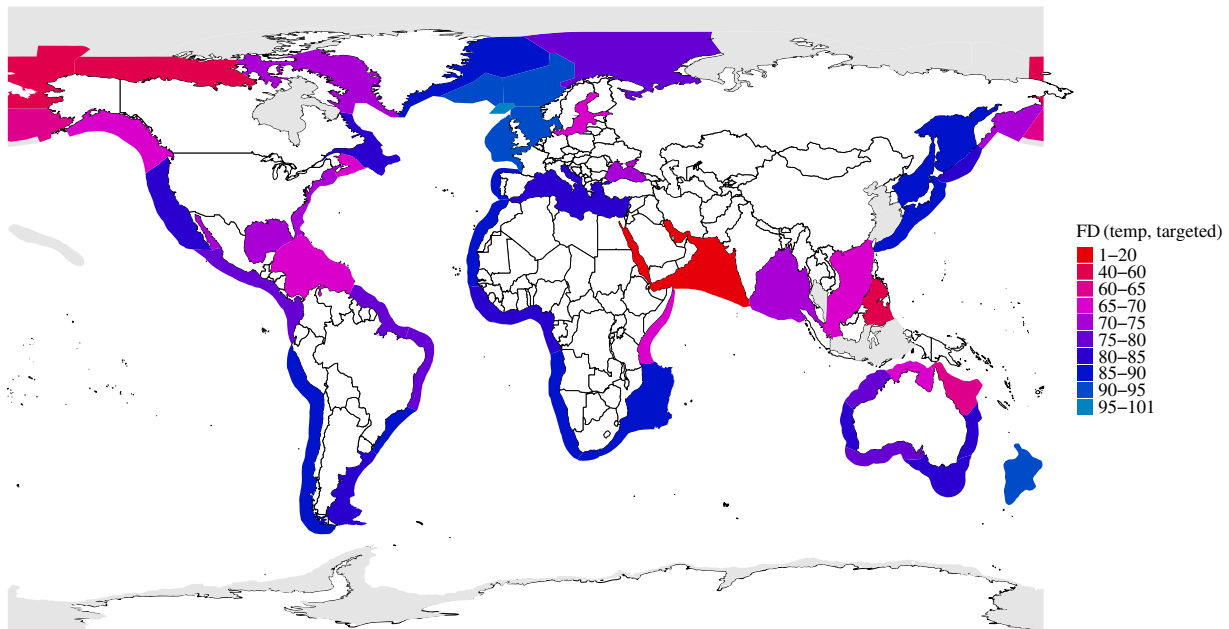
Alternatively, extreme changes in temperature (e.g. heat waves) within a year, which will be reflected in higher within-year variability, can affect yields in several ways. For instance, abnormally high temperatures during the Fraser River's 2004 salmon run increased salmon mortality affecting yields [3]. Extreme temperature events within a year can also alter the



**Figure 1.** Conceptual figure mapping characteristics of thermal performance curves (TPCs) across species to FD, here measured as functional dispersion. TPCs relate environmental temperature ( $T$ ) to measures of performance; we show *per capita* growth rate  $r$  as an example. TPCs dictate that an individual of a species has a temperature optimum ( $T^*$ ) yielding highest performance and a maximum and minimum temperature beyond which growth ceases. (a) Species A, B and C differ in their temperature optima ( $T^*$ ) and range, i.e. minima ( $T_{\min}$ ) and maxima ( $T_{\max}$ ). Note that temperature variability (e.g. between  $T_{\min}^C$  and  $T_{\max}^C$  in a year) positively influences average growth of species C but negatively affect average growth of species A & B for the year. (b) How these parameters, which affect the shape of a species' TPC, can be interpreted as 'traits' characterizing a species' response to temperature fluctuations. These traits, or suitable proxies, can be used to compute the functional dispersion of the set of species (e.g. A, B and C). Functional dispersion measures the mean distance ( $Z$ ) between a hypothetical 'average' species (centroid) and each species in the community.

timing of developmental and behavioural events [13], such as migrations [30], in some cases with positive consequences for yields. For example, in the Gulf of Maine, a heat wave prompted phenology changes that anomalously increased yields [13]. Lastly, large fluctuations in temperature within a year are associated with local weather conditions that can alter the amount of fishing that occurs (e.g. due to safety concerns), and impact yields. Although within-year temperature variability can either increase or decrease annual yields depending on the mechanism and species, we hypothesize that for species adapted to the mean temperature in an ecosystem, greater temperature variability within a year will, on average, reduce yields.

Research in other systems suggests several reasons why diversity in the number of species could mediate the impacts of temperature variability on yields. Harvesting more species (greater species richness (SR)) can positively influence yields through a 'sampling effect': increasing the likelihood of catching a species that is less negatively affected by variation, which helps buffer decreases in yields when temperature variability is higher [18]. Harvesting more species also increases the likelihood of catching some species that benefit from an increase in within-year temperature variation, such as when their performance or productivity is limited by cold temperatures (figure 1).



**Figure 2.** FD of targeted species by large marine ecosystem (LME), measured as the functional dispersion of maximum depth and habitat association, which serve as proxies for temperature range traits (see Methods and electronic supplementary material, appendix). Functional dispersion metrics were scaled between 1 and 101.

The effect of diversity could also be driven by differences in the characteristics of species' thermal responses, regardless of the number of species harvested. Such differences can lead to reduced or even negative correlations in harvests across species and thus lower variance of aggregate harvest via a portfolio effect (e.g. [31]). Rather than focusing on variance of yields, we examine how aggregate yield might be affected by diversity in thermal characteristics. When species respond asynchronously to environmental fluctuations, this negative covariance can increase average biomass of a community available to harvest [15]. We suggest that differences in species' thermal responses could be one mechanism leading species' biomasses to respond asynchronously to temperature fluctuations. For instance, resource-competition models predict that diversity in the location of optima can result in higher overall community biomass because of greater 'coverage' of possible environmental conditions [16,17]. With greater coverage of conditions due to diversity in temperature optima (figure 1), some species will be positively impacted during a year when conditions vary, thereby increasing aggregate yield. Harvesting a more thermally diverse set of species is more likely to include species with different optimal temperatures, giving rise to these yield-boosting effects (figure 1). If all species have the same thermal characteristics, their responses to temperature will be perfectly positively correlated, so harvesting more species would have no effect on yields (following [15]).

In this paper, we examine how *within*-year temperature variability influences aggregate fishery yields and how SR and functional diversity (FD) alter this relationship. We use FD to capture differing responses to temperature variability. In contrast to SR, which treats species as functionally identical, FD measures differences between species based on the values of particular traits [32]. FD estimates depend on the metric choice and traits included (reviewed in [33]); therefore, proper inference requires measuring FD using hypothesis-relevant traits and appropriate metrics [34]. To reflect how species experience short-term temperature fluctuations, we measure FD using traits that relate to species' responses to temperature (i.e. optima, tolerances and/or critical limits; figures 1 and 2). Our

analyses test hypotheses about how within-year temperature variability and its interaction with diversity affect yields, rather than to explain the overall variation in annual yields. We hypothesize that temperature variability will decrease aggregate yields and that harvesting a larger number of species—or species with more diverse thermal response characteristics—will mitigate that effect. In particular, for FD, we hypothesize that the harvested species FD, measured by traits that reflect species' thermal responses (figures 1 and 2), buffers the effect of temperature variability on total yields.

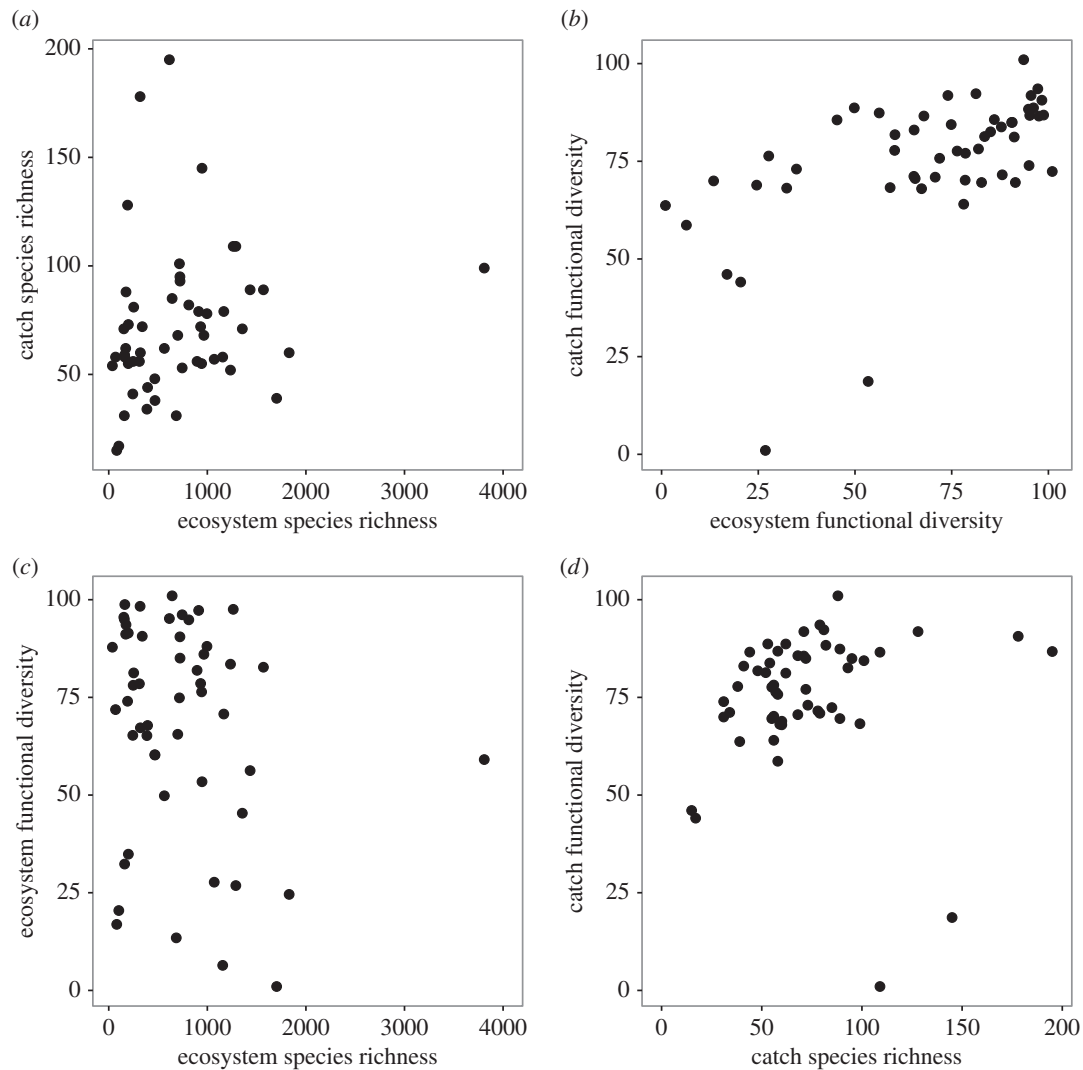
## 2. Material and methods

### (a) Fisheries longitudinal data

With a global time-series of fisheries yields, we ask: (i) does within-year temperature variability impact the annual levels of regional fisheries yields, and (ii) if so, can SR and/or FD mediate the effects of this temperature variability on aggregate yields? We estimate longitudinal (panel) models of total annual fisheries yield from 1982 to 2006 in 53 ocean regions. These large marine ecosystems (LMEs) delineate areas from the coast to the continental shelf based on shared ecological and hydrodynamic characteristics [35]. Due to incomplete or unreliable catch or environmental data, we excluded several LMEs from the analysis: Antarctica, Hudson Bay, Arctic Ocean, Arctic Archipelago, Baffin Bay/Davis Strait, Insular Pacific-Hawaiian, Gulf of Thailand, Indonesian Sea, East China Sea, Yellow Sea, East Siberian Sea, Laptev Sea and the Kara Sea (e.g. [36]). We model total yields across all species in an LME and year as a function of within-year temperature variability and its interaction with biodiversity, while controlling for other factors known or posited to influence fisheries yields as described below (electronic supplementary material, appendix, data appendix and table S1 further describe the dataset). Global catch and temperature data availability determined the study window.

### (b) Isolating the effect of within-year temperature variability and diversity on yields

Total yields vary across LMEs for many reasons other than diversity or within-year temperature variability. Given our focus on



**Figure 3.** Relationships between the diversity of the catch versus the ecosystem (all fish species) and the diversity metrics we used, species richness (SR) and FD, for the 53 large marine ecosystems in the analysis. FD scores were scaled between 0 and 101. (a) SR of the ecosystem and SR of the targeted species are not meaningfully correlated ( $r = 0.191$ ). (b) FD metrics calculated for the ecosystem versus the FD of the targeted species are also not highly correlated ( $r = 0.556$ ). No significant relationships were found between (c) SR and FD of the fish in the ecosystem ( $r = -0.204$ ) or (d) SR versus FD of the targeted species ( $r = 0.072$ ).

estimating how within-year temperature variability and biodiversity jointly impact yields, rather than explaining variation in total yields, we control for other factors that drive yields. For controls, we include covariates known to influence yields and with time-varying, LME-specific information (e.g. individual quota (IQ) programmes, marine protected areas (MPAs), number of stock assessments and upwelling potential).

Several other factors can also drive yields but are unobservable or lack reliable data for all LMEs in the analysis. To control for variation in yields due to such factors, in all of our models, we estimate a separate intercept and polynomial time trend for each LME by including an LME dummy variable and its interaction with a polynomial in the number of years since 1982 (see equation (2.1)). Including those terms is equivalent to removing both LME-average yields and trends from the data, and studying how the variables of interest affect the remaining deviations from those trends. Per-LME intercepts control for baseline differences in LMEs and unobservable, time-invariant, region-specific drivers of yields, including average productivity, LME size, mean species' length and the probability of fishing sustainably (factors shown to be important in [37,38]). Per-LME intercepts also absorb the direct effect of biodiversity on yields, because our biodiversity measures are time-invariant; therefore, we cannot separately identify a main effect of biodiversity on yields. The per-LME polynomial trends control for other factors affecting yields that change smoothly through time and are not explicitly addressed by our control variables, including

fishing effort and economic development. Furthermore, per-LME polynomials, which include a linear trend, control for effects of smooth trends in mean temperature on yield (e.g. from warming).

### (c) Within-year temperature variability

We estimate the direct effect of within-year temperature variability on yields, while controlling for confounding factors as outlined above. Within-year variability of SST is measured for each year and LME by the coefficient of variation (CV) of monthly temperatures for each  $1^\circ \times 1^\circ$  spatial cell, averaged across all cells in an LME (data from [39]; electronic supplementary material, figure S1). Our results are robust to using an alternate within-year temperature metric: standard deviation of SST (electronic supplementary material, appendix). We also considered lagged SST CV (e.g. which could influence yields through recruitment).

### (d) Diversity metrics and functional trait selection

We test whether biodiversity provides resistance against the effect of within-year temperature variability on fisheries yields by interacting biodiversity and within-year temperature variability. We measure biodiversity as SR and FD, the latter measured as functional dispersion using presence-absence information [40] (figure 1; electronic supplementary material, appendix), for both the targeted species and the ecosystem (all fish species in each LME; figure 3; electronic supplementary material, table S1).

Including ecosystem biodiversity helps separate the impacts of diversifying catch versus a more diverse ecosystem. Our dataset provides time-invariant lists of species present and caught in each LME, so biodiversity measures are constant through time (values shown in figure 2). Owing to trait data availability, we compute FD of fish species only, which comprise the majority of catches (see the electronic supplementary material, appendix).

We measure functional dispersion with respect to traits that act as proxies for species' temperature preferences due to poor global coverage in species' temperature minima and maxima information (electronic supplementary material, figure S2 and appendix; [41]). Specifically, we use maximum reported depth and habitat associations (bathodemersal, bathypelagic, benthopelagic, demersal, pelagic-neritic, pelagic-oceanic and reef-associated) as proxies for temperature minimum and maximum. In testing potential proxies, we found that species' maximum reported depth had the highest correlation with both temperature minimum ( $r = -0.60$ ) and maximum ( $r = -0.67$ ) of all numeric traits with greater than 5% coverage in FishBase (electronic supplementary material, figure S2). Additionally, all habitat association categories were significant predictors of these temperature traits (electronic supplementary material, appendix). Previous studies also suggest maximum depth is a good proxy for minimum temperature ( $T_{\min}$ ) [42], and that habitat association is likely related to optimal temperature ( $T^*$ ) [8]. For species missing information on maximum reported depth or habitat association, trait values were imputed using either the median or mode among similar species (electronic supplementary material, appendix).

Functional dispersion computed with different traits contains different information (electronic supplementary material, figure S3); therefore, we examine the importance of trait selection. As a falsification test, we include a measure of FD based on traits we would not expect *a priori* to influence responses to temperature variation in the current year (species trophic level and trophic level of prey species; electronic supplementary material, appendix). All FD metrics were computed using the FD package in R [40] and are scaled between 1 and 101 so that the log of the least functionally diverse system is zero, simplifying coefficient interpretation.

### (e) Statistical model

We estimate models of the form

$$\log(Y_{it}) = \alpha_i + P_i(t - 1982) + \beta_T V(T_{it}) + \beta_{BD} V(T_{it}) \cdot \log(BD_i) + \gamma X_{it} + \varepsilon_{it}, \quad (2.1)$$

where  $Y_{it}$  is total yield in LME  $i$  in year  $t$ ,  $V(T_{it})$  represents within-year temperature variability,  $BD_i$  is a vector of biodiversity metrics,  $X_{it}$  is a vector of other explanatory variables and  $\varepsilon_{it}$  is an error term. Other explanatory variables are number and the presence/absence of IQ programmes [43] and of MPAs [44], number of stock assessments as a proxy for use of science to guide management [45,46] and upwelling potential (mean minus minimum SST, electronic supplementary material, appendix). To control for additional confounding factors, as described above, we account for baseline differences across LMEs through an intercept per-LME  $\alpha_i$  (time-invariant) and use per-LME polynomial time trends  $P_i(t - 1982)$  to control for determinants of fisheries yields that change smoothly through time in each region.

From equation (2.1), the effect of an increase in within-year temperature variability on catch will depend upon biodiversity

$$\frac{\partial \log(Y_{it})}{\partial V(T_{it})} = \frac{\partial Y_{it}/Y_{it}}{\partial V(T_{it})} = \beta_T + \beta_{BD} \cdot \log(BD_i). \quad (2.2)$$

The signs of  $\beta_T$  (for within-year temperature variation) and each coefficient estimate of  $\beta_{BD}$  (for biodiversity metrics) will determine whether the corresponding type of biodiversity dampens or magnifies the effect of an increase in within-year temperature

**Table 1.** Regression estimates for model of log total annual fisheries yields (in tonnes) by LME from 1982 to 2006. Coefficients corresponding to our main hypotheses are significant ( $p < 0.05$ ) and italicized. This model specification (equation (2.1)) includes per-LME intercepts and cubic time trends per-LME (estimates omitted for brevity). All standard errors are cluster robust. MPAs, marine protected areas; IQs, individual quota programs; FD, functional diversity; SR, species richness. BIC: 219.0, Adj.  $R^2$ : 0.994.

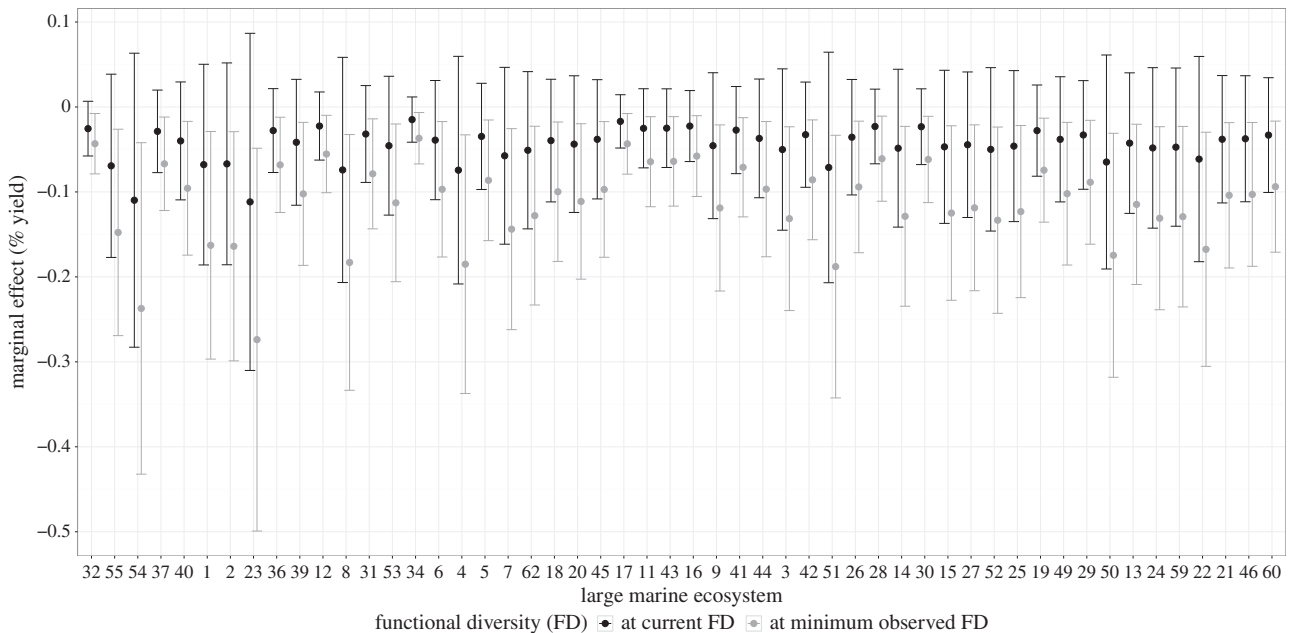
	estimate	s.e.	<i>p</i> -value
<i>SST CV</i>	-146.73	61.59	0.017*
<i>SST CV: (log) temperature</i>	20.58	4.93	<0.001***
<i>FD catch</i>			
SST CV: (log) SR catch	28.5	21.32	0.182
SST CV: (log) temperature	-18.79	14.27	0.188
<i>FD all fish</i>			
SST CV: (log) SR all fish	2.54	9.39	0.787
SST CV <sub>t-1</sub> (lagged effect)	5.59	10.95	0.61
MPAs (yes/no)	-0.08	0.23	0.715
(log) no. MPAs	0.07	0.08	0.434
(log) no. Stock assessments	-0.15	0.11	0.175
IQs (yes/no)	0.21	0.07	0.005**
(log) no. IQs	-0.04	0.04	0.246

variability on catch. Coefficients of  $\beta_{BD}$  with a sign opposite to  $\beta_T$  indicate dampening effects. Because biodiversity measures are time-invariant, their main (and thus total) effect cannot be identified separately from the per-LME intercepts. Thus, our results and interpretation focus only on the role of biodiversity in buffering temperature variability effects.

We examined the robustness of our results by including alternate time trends (cubic versus quartic), indicators of upwelling (ocean productivity) and examining different approaches to fill in missing trait values (electronic supplementary material, appendix). We compared models using Bayesian information criterion (BIC) and selected the model with the best (lowest) BIC, which we refer to hereafter as the 'preferred model' (table 1). Using coefficient estimates of significant variables from the preferred model that relate to our hypotheses, we calculate and interpret marginal effects of an increase in temperature variability on yields under two scenarios, with catch FD: (i) at existing levels and (ii) reduced to the lowest FD level observed in any LME. In both cases, we consider an increase in temperature variability equal to the average year-to-year change in SST CV in each LME. We subtract those two marginal effects to estimate how much catch FD buffers the effect of the temperature variability on yields (details in the electronic supplementary material, appendix). This calculation does not give the total effect of a change in catch FD but does indicate how much the loss in yield due to temperature variability can be dampened if fishing targets a more functionally diverse set of species.

## 3. Results

Within-year temperature variation significantly and negatively affects total annual yields within an LME, consistent with our hypotheses (table 1). Similarly, we found consistent evidence that FD of the set of harvested species can mediate the negative impacts of within-year temperature variability on yields



**Figure 4.** Marginal effects of temperature variability on fisheries yield per large marine ecosystem (LME) at current levels of catch FD (black) and at the lowest level of catch FD observed in our dataset (grey), which was in the Red Sea LME. Catch FD is measured using the temperature-related trait set, and reported effects are per cent changes in yield. Error bars indicate 95% CIs for predictions. Magnitudes of these marginal effects and a key for LME numbers are presented in the electronic supplementary material, table S4. LMEs are ordered from lowest to highest FD (left to right).

(table 1;  $\beta_{\text{FDcatch}} = 20.58$ ,  $p \leq 0.001$ ), holding SR constant. By contrast, we did not find robust evidence that SR of the catch had a significant effect. This finding is consistent with figure 3*c,d*, which shows that SR and FD metrics contain different information. Furthermore, the effect of FD depends on which traits were included; FD computed with traits that are relevant to temperature fluctuations had a significant effect, while FD with traits with no *a priori* expectation to determine species' responses to temperature fluxes did not (electronic supplementary material, figure S3 and table S2).

In contrast to FD of the catch, FD of the ecosystem when interacted with temperature variability had a negative effect (table 1;  $\beta_{\text{FDe}} = -18.79$ ,  $p = 0.19$ ), which was significant in some models (electronic supplementary material, table S3). We did not find evidence that SR of the ecosystem had effects significantly different from zero in any model (table 1; electronic supplementary material, table S3).

The FD of targeted species can offset the negative effects of current levels of temperature variability (figure 4). If FD of targeted species in every LME were reduced to the lowest level observed in any LME, our model predicts that temperature variability would lead to an additional decline in global yields of 6.8%, or on average 68 000 tonnes per-LME and year, given average levels of temperature variability in each LME (figure 4; electronic supplementary material, table S4). The Humboldt Current would experience the largest average losses: -616 000 tonnes per year (95% CI =  $\pm 289\,000$  tonnes; 7% loss) based on average catch per year from 1982 to 2006. The Beaufort Sea would have the smallest absolute effect (-22 tonnes per year; 95% CI =  $\pm 10$  tonnes; 8% loss). The magnitude of these predicted losses for each LME depends on the levels of historical within-year temperature variability and FD of the targeted species, which vary by region (electronic supplementary material, table S4). These predictions assume the estimated marginal relationships hold over a large range of FD and therefore should be interpreted as approximations only. Finally, we emphasize that

these predictions reflect only the partial effect of FD on yields through buffering temperature variability impacts.

None of the alternate models considered substantively affect the results or coefficient estimates of interest; the coefficient estimates of interest were consistent across all model specifications (electronic supplementary material, table S3). We found no evidence that lagged within-year variability affected yields, and including upwelling potential in our model did not change our main results (electronic supplementary material, table S3). Our results were also robust to multiple approaches for filling in missing trait values (electronic supplementary material, appendix and table S5).

## 4. Discussion

This study fills an important research gap by jointly considering ecosystem services (i.e. fisheries yields), biodiversity, and the effects of variable temperatures over short, within-year time-scales [47]. Connecting these sub-disciplines provides new insights about the consequences of short-term temperature variation for fisheries yields and the role of FD in reducing these impacts. To our knowledge, we provide the first empirical evidence that FD in thermal characteristics lessens the negative impacts of within-year temperature variability on fisheries' yields, thereby raising aggregate yields in the face of within-year temperature variability.

As hypothesized, higher temperature variability within a year negatively impacts average yields; however, the magnitude of this impact is smaller in regions with greater FD of targeted species. Specifically, our analyses provide evidence that FD in traits that act as proxies for species' thermal characteristics can mitigate effects of within-year temperature variation on total yields, after controlling for SR (table 1 and figure 4). This result suggests that during years with more variable temperatures—or if within-year temperature variability

increases with climate change—FD in thermal characteristics of targeted species could be even more important.

Whether and how biodiversity affected the level of fisheries yields depended heavily upon how diversity was measured and for what collection of species. Of the aspects of biodiversity considered, only FD of the target species—measured with traits related to thermal performance—consistently had a significant and positive interaction with within-year temperature variability (table 1; electronic supplementary material, tables S2 and S3). By contrast, FD of the ecosystem (all fish species) compounded the negative effect of temperature variability, and significantly in some models (electronic supplementary material, table S3). One explanation for this result is that increasing FD of non-targeted species could allow these species to outcompete target species for resources under more variable conditions. Furthermore, FD of the target species only mediated temperature variability effects if measured with traits related to their potential responses to temperature (electronic supplementary material, table S2), corroborating our interpretation of the results. Together, these results highlight the importance of measuring biodiversity using sets of species, metrics and traits that reflect the pathways through which biodiversity influences ecosystem services like fisheries.

This study differs from prior work on biodiversity and global fisheries by testing hypotheses about how biodiversity mediates the impacts of temperature variability on the level of yields. Previous studies examined a reduced-form relationship ('main effect') between biodiversity and global yields and only used measures of SR (not FD) [37,48]. While Worm *et al.* [48] found that ecosystem SR was positively correlated with average yields of non-collapsed stocks, Chassot *et al.* [37] found no evidence that SR of the ecosystem contributed to productivity of yields. We also found no evidence that SR of the ecosystem offsets negative impacts of within-year temperature variability. Furthermore, Worm *et al.* [48] concluded that the SR of the catch had a positive correlation with total catch levels, whereas we did not find robust evidence that SR reduced the negative impacts of within-year temperature variability on total annual yields (yields summed across species; table 1; electronic supplementary material, table S3). Importantly, these results are not incompatible: the SR of the catch could impact aggregate yields through a mechanism other than by reducing the impact of temperature variability.

Our results complement existing studies applying portfolio theory to fisheries. Portfolio theory predicts that variability in yields will be dampened when yields across species or populations are not perfectly correlated. Empirical studies support this hypothesis: population diversity within a salmon species (*Oncorhynchus nerka*) gives rise to imperfect correlation [49], which lowers variability in aggregate yield over time [31,50]. Although we do not explicitly test for a portfolio effect by assessing variance in yield, we identify an empirical link between FD (of the catch) and the *amount* of yields, in line with a 'performance-enhancing' effect of diversity [15]. We hypothesize that by buffering the negative impacts of within-year temperature variability on *average levels* of yields, diversity in thermal characteristics may simultaneously reduce variance in yields.

Our analysis suggests several promising new research directions. First, while we examined how within-year temperature variability affects yields, variability at other

timescales might also impact yields both directly and in interaction [3,10,11,51]. Our empirical approach controls for longer-term temperature trends but does not study them directly. Increases in mean SST are already reducing some species' growth rates [28], shifting distributions of stocks [52], changing species' phenology [13,30], and spatially redistributing yields [53]. Yet, many of these studies do not directly address the interaction between mean temperature and temperature variation. As the climate changes, the consequences of changing temperature variability may depend upon the shifts in mean temperature and *vice versa* [11,54]. Furthermore, short-term variability within a growing or reproductive season might impact a species' ability to acclimatize to longer-term warming. Even within a population, selection in a highly variable year could make the population ill-adapted to a low-variability year in the future, or *vice versa*. Interactions between changes in the mean and variance of temperature may also be important for the relationship between diversity, temperature and yields, especially when these shifts favour the production of different species. Forecasting consequences of climate change, and estimating other ways that diversity may be important, will require a better understanding of how short-term variation couples to longer-term variation and trends in temperature.

Second, further research is needed to elucidate the underlying mechanism(s) for why temperature variability negatively affects yields and why higher FD in the catch offsets that effect. Harvesting species with different temperature optima could lead to that observed result. Alternatively, human behaviour could drive the result: harvesting a thermally diverse set of species enables fishers to target species better suited to the current temperature regime, either passively or actively. Fishers using non-selective gear like trawl nets would passively benefit from thermal FD by capturing the most productive species for a given regime. Or, fishers can shift effort among fisheries or locations to target different productive stocks under different temperature regimes [13]. Another possible explanation is that species with high thermal tolerances are driving higher FD, based on how we measured FD (electronic supplementary material, figure S4); distinguishing between effects from thermal breadth and diversity in optima requires more detailed data. Overall, determining which mechanisms are responsible for the relationships we found is an important next step and will require developing approaches to isolate these mechanisms at management-relevant scales (using observational datasets).

Our findings have implications for fisheries management. Most management rules ignore both temperature variability and FD, suggesting some scope for improvement in management. For example, managers could actively buffer yields in the face of seasonal temperature variability by regulating harvest to target a portfolio of species with diverse thermal performance characteristics. Management institutions could alter catch limits or control how harvesters dynamically reallocate their effort to different species based on observed environmental conditions. Managers could also encourage individual fishers to diversify which species they target—among commercially valuable species—according to thermal characteristics. Prior work identified that permit diversification reduces financial risk and variability in fishers' revenue [55]. Here, we suggest holding a 'thermally diverse' set of permits is a way to reduce financial risk when facing variable temperatures in a year. This strategy will allow fishers to more readily switch among



productive stocks, which the current structure of most commercial fisheries management does not accommodate [13]. However, diversifying target stocks might have other effects on yields, which, if undesirable, would have to be weighed against the benefits from buffering temperature variability.

## 5. Conclusion

Understanding how climate impacts populations and the ecosystem services they provide is a key research area at the nexus of ecology and climate science. Our analyses suggest that within-year temperature variability has a negative impact on regional fisheries yields, but that FD of the harvested species helps mitigate this impact. Despite the potential importance of variability for populations and communities, most natural resource management does not include such considerations, especially the effects of short-term variation. Based on our findings, management strategies that take advantage of FD to help enhance and protect ecosystem service provisioning, such as encouraging fishers to hold permits for diverse stocks, could maintain more productive services into the future. Given that

environmental variability is predicted to change in many places as our climate changes [56], there is a need for scientists and managers to place more emphasis on understanding the effects of short-term variability on the provisioning of ecosystem services.

**Data accessibility.** Data are available as an electronic supplementary material.

**Authors' contributions.** L.E.D. conceived of the study with input from all authors; L.E.D., R.S., S.J.M. designed the empirical analyses; L.E.D., S.J.M., L.E.P. processed data; L.E.D. and S.J.M. performed the analyses; L.E.D. wrote the paper with contributions from all authors. All authors approved of the final version.

**Competing interests.** We declare we have no competing interests.

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