# Thermal biases and vulnerability to warming in the world's marine fauna

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## Summary

A critical assumption underlying projections of biodiversity change associated with global warming is that ecological communities comprise balanced mixes of warm and cool affinity species which, on average, approximate local environmental temperatures. Nevertheless, we find most shallow water marine species occupy broad thermal distributions that are aggregated in either temperate or tropical realms. These distributional trends result in ocean-scale spatial thermal biases, where communities are dominated by species with warmer or cooler affinity than local environmental temperatures. We use community-level thermal deviations from local temperatures as a form of sensitivity to warming, and combine these with projected ocean warming data to predict warming-related loss of species from present-day communities over the next century. Large changes in species composition at the site-scale appear likely, and proximity to thermal limits, as inferred from present-day species' distributional ranges, outweighs spatial variation in warming rates in contributing to predicted rates of local species loss.

## Main text

The inherent vulnerability of ecological communities to global warming, and therefore the magnitude of associated biodiversity change, is considered a function of exposure and sensitivity to warming, coupled with species' adaptive capacity[1-3]. Geographic models of future biodiversity change generally accommodate the magnitude, direction and distribution of temperature change[4-8], but have limited ability to account for sensitivity. Our understanding of sensitivity to warming has been largely based on results of comparative studies of species physiological tolerances and other life-history traits, often with extension from the laboratory to the field[9-12]. Extrapolation to whole ecological communities and large geographic scales, does, however, introduce substantial uncertainty, yet these are the scales critical for understanding natural ecosystem functioning[13], on which the well-being of human society depends.

The few studies that have considered community-level sensitivity to warming[3,7,14] have not accounted for geographic patterns in species distributions, inherently assuming that communities comprise balanced mixes of relatively warm and cool affinity species, and with no spatial trends or regional consistency in any deviation from this. Regional variation in species composition may be influenced by numerous historical, ecological and phylogenetic factors that could potentially result in thermal bias of communities in relation to local environmental temperatures, with important implications for community-level sensitivity to warming. If, for instance, most species have a warmer affinity than the mean local temperature, then the local community may have little intrinsic sensitivity to negative change with warming. In this case, proxies previously used for inferring sensitivity, such as habitat type or integrity[3], may provide limited predictive insight. Quantifying the direction and magnitude of community thermal bias is therefore an important step in improving our understanding of the sensitivity of ecological communities to structural reorganisation with warming, and providing a more direct means to account for sensitivity in predictions of vulnerability.

## Thermal Biogeography

The Community Temperature Index (CTI) is a measure (a community-weighted mean) of the average thermal affinity of ecological communities, and has recently been used to quantify warming in birds[15,16], butterflies[17] and fishes[18], and global commercial fisheries catches[19]. Here we use the CTI of shallow water marine fishes and invertebrates to test for thermal bias in the global distribution of marine communities in relation to local environmental temperatures.

We constructed geographic and thermal distributions for 2,695 reef fish and 1,225 mobile macroinvertebrate species using occurrence records from two of the world's most comprehensive databases for shallow water marine species (Global Biodiversity Information Facility, www.gbif.org, and Reef Life Survey[20,21], www.reeflifesurvey.com), combined with remotely sensed long-term mean sea surface temperature[22]. We used the midpoint of the realised thermal distribution as a measure of the central thermal tendency for each species, or thermal affinity. On average, this aligns with the temperature at which species occur at their maximum abundance in the field (see methods), and is therefore a good proxy for the temperature of a species' maximum ecological success.

We then compiled the first global-scale dataset of abundance-weighted CTI values from systematic quantitative sampling, using abundance data for all fish and invertebrate species recorded on standardised visual censuses at 2,447 sites by the Reef Life Survey (RLS) program (see methods; ED Fig 1). This approach thus incorporates patterns in species' dominance related to thermal affinity.

A non-linear global pattern is evident in CTI values, with relatively little change with increasing temperature in tropical and temperate regions, and a rapid increase in subtropical regions creating a distinct step (Fig 1; ED Fig 2a, b). This pattern is consistent between fishes and invertebrates (Pearson correlation = 0.98; n = 2,383; $p<0.01$) and is the same when CTI is calculated without weighting by abundance (i.e. using presence data; ED Fig 2c, d). A direct result of this non-linearity in global CTI is that the majority of locations are characterised by marine communities with either higher or lower CTI than would be expected from local SST (ED Fig 3). Thermal bias is ubiquitous among these communities, which are typically numerically dominated by species with warmer or cooler affinity than the local environment.

The proximate cause of large-scale patterns of thermal bias is that marine species distributions do not follow the monotonic latitudinal and temperature gradients observed in species richness[23,24]. Instead, we find that the majority of species studied have ranges centred in either temperate or tropical zones (ED Fig 4), and consequently show a corresponding multimodal distribution of the thermal affinities (i.e. thermal guilds; Fig 2). This trend is consistent when considered for different ocean basins and biogeographic regions. Additional to the major temperate/tropical dichotomy, the invertebrate data suggest the presence of a third, sub-polar thermal guild (Fig 2b).

Thermal guilds align with the theory that temperature can be considered as an ecological resource in freshwater fishes[25], and can be distinguished within other independent datasets of marine species (see Supplementary Information). The findings of globally coherent thermal guilds is not the result of spatial sampling structure of the data, such as a consequence of relatively few surveys in the subtropics; a latitudinal transect along the well-surveyed north-south trending eastern Australian seaboard clearly distinguishes tropical from temperate faunas along the full cline (ED Fig 5). There are several potential, non-mutually exclusive mechanisms that may explain these findings: (a) Fewer shallow water species may have ranges centred in subtropical ocean climates as a result of less continental shelf area at subtropical latitudes globally[26]; (b) Historical biogeographic processes could be implied for the Australian fauna, through mixing of tropical Pacific/south-east Asian and temperate Australian faunas as the Australian continental plate drifted north, with species conserving thermal preferences (i.e. phylogenetic inertia[27]); (c) Tropical centres of speciation and subsequent colonisation of temperate regions through ‘bridge species’ may have occurred (the ‘out of the tropics’ hypothesis[26]), and is supported by the distributions of thermal affinities of species in large families of fishes that span temperate and tropical zones (ED Fig 6); (d) There could be adaptive advantages associated with specialisation for either warm or cool temperature ranges, with trade-offs in metabolic processes reducing widespread adaptation to intermediate temperatures.

Regardless of the ultimate divers, the existence of consistent thermal guilds and associated global-scale patterns of thermal bias has implications for whether the net community response to warming is more likely to be positive or negative (in terms of abundance changes). It also raises the possibility that communities in some locations may be more vulnerable to losing species than in other locations, simply on the basis of the direction and magnitude of the bias in the thermal distributions of the species present.

## Vulnerability of marine communities to warming

Most previous biodiversity vulnerability analyses have focussed on species, and their ability to change their geographic distribution or adapt to avoid global extinction[10,28]. Here we quantitatively assess the vulnerability of whole communities - groups of species that are currently recorded as co-occurring and interacting at an ecologically-relevant scale. A local ecological community is considered vulnerable if it is likely to lose many of its constituent species. This may not translate to reductions in overall species richness (although see below), but does reflect a relative vulnerability to change in community structure and ecosystem functioning, and contrasts with desirable management goals of resilience or stability in the face of warming[29].

Over decadal scales, positive thermal bias of the magnitude observed for some locations in this study (e.g. where the mean thermal affinity of the community is 3°C greater than local mean SST) is much greater than predicted ocean warming rates of <0.4°C per decade, and could be interpreted to translate to low probabilities of species loss as a result of warming, or relatively low community sensitivity to negative change. Most species in such locations are also found in other warmer locations, and so are unlikely to be negatively affected by warming. However, the likelihood of local loss of species on the basis of increasing temperature will be more dependent on how close each of the species is and becomes, at that location, to the maximum of its thermal distribution, rather than from the midpoint (as used to define thermal bias in our thermal biogeographic analysis). To account for this, we recalculated CTI using the 95th percentile of species' thermal distributions as a measure of contemporary realised upper thermal limits ($CTI_{max}$). Realised upper limits will be lower than fundamental limits based on physiological tolerances, but arguably better reflect real world limits, where species not only need to survive physiologically, but also persist in a competitive and predatory environment.

For calculation of $CTI_{max}$ to estimate species loss with warming, we used presence rather than abundance data and combined RLS survey data for fishes and invertebrates, thereby covering the majority of macroscopic mobile fauna (>2.5 cm) on rocky and coral reefs at sites investigated. We re-calculated thermal bias ($TBias_{max}$) as the difference between $CTI_{max}$ and mean summer temperatures (mean SST from the 8 warmest weeks annually from 2008-2014[30]). This can be considered a form of 'distribution safety margin'[27], and shows a similar global pattern to that shown in our thermal biogeographic analysis (ED Fig 7), with $CTI_{max}$ and CTI very closely related (Pearson correlation = 0.96; n = 2,089; $p<0.01$).

$CTI_{max}$ also shows a stepped relationship with summer SST (ED Fig 8), reflecting some consistencies among species' realised upper thermal limits within tropical and temperate regions at the global scale. For example, $CTI_{max}$ remains between 22°C and 24°C across most sites with summer temperatures ranging from 14°C to 24°C, implying that the average species is living closer to their warmest distributional margin at locations with summer temperatures ca. 24°C than at locations which experience summer temperatures ca. 14 °C. $TBias_{max}$ is consequently more positive for the latter, although sites dominated by species in the tropical thermal guild (as identified in Figs 1 and 2) that experience summer temperatures ca. 24°C (i.e. on the upper step of ED Fig 8) also have high $TBias_{max}$ and inferred low sensitivity.

While TBias$_{max}$ can be considered a form of community-level sensitivity, it does not account for warming rates, another important component of vulnerability[1,2]. To explicitly account for spatial patterns in warming rates and provide quantitative vulnerability predictions for marine communities, we further calculated the proportion of species in the community that would exceed the upper limit of their realised temperature distribution in 10 and 100 years from present. These are based on each species' contemporary upper thermal limits, recent summer temperatures, and the rate of warming expected at each site (based on ensemble averages from all climate models included in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (AR5) for sea surface temperature anomaly under the RCP8.5 scenario predicted for 2050-2099; http://www.esrl.noaa.gov/psd/ipcc/).

Six of 75 ecoregions included in the analysis are identified in which the mean summer sea temperature is expected to exceed the upper thermal limit of more than 50% of species recorded by 2025 (Fig 3a, b). Confidence scores for CTI$_{max}$ values are low for a number of sites in three of these ecoregions on the basis of less comprehensive sampling of species thermal distributions (see methods and ED Table 1), but were high for sites in the Gulf of Thailand, Southwestern Caribbean and Three Kings-North Cape (NZ). Longer-term predictions are more extreme, with 100% of the present-day community composition apparently likely to exceed upper thermal limits in approximately one-third of surveyed ecoregions by 2115 (Fig 3c, d). These are distributed in all ocean basins across the tropics, but also in some temperate areas such as the Great Australian Bight.

Locations of greatest predicted species loss do not closely align to locations of greatest warming, but instead correspond closely to the magnitude of thermal bias (measured as TBias$_{max}$; Fig 3 b, d; GAMM results in ED Table 2). This result is robust to the warming data used (See Supplementary Information), and shows that sensitivity associated with community thermal bias is an important component of vulnerability. Our results further indicate that exposure, and variability in warming rate predictions, may be considerably less important than previously suggested[1] when it comes to local loss of marine species over the next century. Predicted species loss at locations with lower thermal bias is considerably greater than at locations with higher thermal bias, despite some of the world's most rapidly warming regions occurring within the latter. The western Mediterranean, for example, is predicted to warm by 0.24-0.29°C per decade (depending on predictions used), but typical marine communities there consist of species with contemporary upper limits well above local summer SST (mean $TBias_{max}$ = 6.3°C ± 1.1SD).

Our predictions do not account for local influx of warmer affinity species, and do not comprise the only form of community-level vulnerability to warming. Rather, they describe impacts of an additional component of ecological vulnerability. Species influx and warming-associated changes in species abundances will also contribute to local ecological change and are already occurring in the most rapidly warming areas that are well-connected to rich tropical faunas, such as south-eastern Australia[12]. Influx of warm affinity species may replace lost species, or lead to accumulating richness in some regions, and likely have dramatic impacts on ecological processes[6,31]. Local species loss through extinction or range contraction will represent the main form of community change likely for low latitude regions for which no pool of warmer affinity species exists[11,32], however, and so our predictions likely cover the major changes in composition expected in these regions.

A key assumption for our vulnerability analysis is that local extinction becomes more likely when a site becomes warmer than the typical maximum temperature at which a species has previously been observed. This assumption relies on the interactive mechanisms which presently set boundaries on species' ranges remaining consistent, such as thermally-driven performance reduction[33,34] and increased susceptibility to competition and predation[18,35]. This is unlikely true for all species, especially narrow range endemics which are probably limited in distribution by factors other than temperature[12]. Regardless, we consider this generalisation reasonable in light of the well-connected nature of the marine environment, typically large geographic ranges[36], and often closely matching fundamental (assessed in laboratory experiments) and realised (field-derived from distribution data) thermal niches[37], as well as implications associated with lower concentrations of dissolved oxygen in the marine environment with increasing temperature[38].

Our vulnerability predictions also do not account for ecological change resulting from extreme events, which will change biodiversity in spatially variable and largely unpredictable ways. This is particularly true for indirect effects of extreme events, such as through habitat change, which place critical pressures on biodiversity[39], and represent an important direction for future research.

Additional caveats associated with assessing vulnerability in terms of local loss of species from present-day communities include: (1) the upper thermal limits for many tropical marine species could exceed contemporary ocean temperature maxima, and (2) adjustment and thermal adaptation could reduce species loss from that predicted. The former does not affect results for temperate regions, but could lead to lower vulnerability than predicted for tropical regions, despite results of laboratory experiments that have applied greater temperatures than contemporary SST suggesting that maximum thermal tolerance levels are more constrained for tropical than temperate species[11,27,40]. Because of these caveats, we emphasise that absolute values presented in Figure 3 should be considered as a ‘worst case scenario’ and interpreted with caution. Nevertheless, relative differences in the magnitude of predicted change between regions and times should be robust, other than perhaps overestimation of site-scale species loss at the lowest latitudes relative to cooler climes. Most importantly, the strength of empirical trends indicates that thermal bias is a fundamental element affecting global variability in future biodiversity change.

## Tracking and managing warming impacts on marine biodiversity

In contrast to prior global studies of potential biodiversity losses associated with climate change, which typically consider loss of species from their full distribution or use regional species lists inferred from range maps, our study focussed on probabilities of local-scale losses from assemblages of interacting species. These will be much more pervasive than cases of global extinction, and have important consequences with respect to the way ecosystems currently function. We identify a substantial pressure of warming through the future, with an alarmingly large proportion of species predicted to exceed current realised thermal limits based on current distribution patterns.

Our results imply that locations at which the average summer SST is presently ca. 24°C are most vulnerable to community change in general. This temperature corresponds to the upper realised thermal limit of many temperate species, and consequently a ceiling on $CTI_{max}$ for most temperate communities. For locations with connections to tropical faunas, it is also where the influx from the large pool of tropical species is going to be greatest. By contrast, the warmest tropical locations are likely to suffer from local loss of species with little replacement, a result consistent among other studies relating biodiversity change to global variation in predicted ocean climate velocity[4,6].

Management options for decreasing local marine species losses resulting from warming are limited; nevertheless, reducing the impacts of other threats, such as pollution, invasive species, and excessive extraction of living resources, will likely provide the best opportunities for prolonging persistence of species at the warm end of their range. While some local losses of species appears inevitable, management can bolster community resilience to ocean warming through strategies to reduce influx of warm affinity species at those regions where accumulation is predicted. Actions to support more intact naturally-functioning communities are recommended, including implementation of marine protected areas (MPAs) and more conservative fisheries management. Recent evidence from an effective temperate MPA suggests that local predators hinder poleward progression of warm-affinity species[18], and invasion theory more generally predicts intact and diverse natural communities possess greater resistance to invasive species than degraded communities[41].

Abundance-weighted CTI, as used in our thermal biogeographic analysis, offers an important tool for measuring the success of such management actions, as it integrates signals from local species gains and losses, and also abundance shifts related to temperature. The CTI provides a powerful metric for tracking long-term biodiversity change in relation to warming over larger scales[15], and for informing the wider public of the magnitude of warming impacts on biodiversity. It can thus fill a critical gap in the indicator suite used for assessing progress towards international targets agreed under the Convention on Biological Diversity (CBD). However, we must consider for such application that the magnitude of CTI change will be non-linear across latitude, with reduced scope for change in tropical regions. The CTI offers an important opportunity to extend emphasis from charts or maps of pressures, such as atmospheric $CO_2$ concentrations and ocean heat content[42], towards measures of real biodiversity change, thereby providing a better understanding of on-ground consequences of ocean warming for effective long-term change in policy and behaviour.

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## Author contributions

RDSS, AEB and GJE conceived the idea, GJE, RDSS and many others collected the data. RDSS drafted the paper, with substantial input from all other authors. SJK prepared the maps, AEB and RDSS analysed the data and prepared figures. Reprints and permissions information is available at www.nature.com/reprints. A 'live' (periodically updated) database containing the Reef Life Survey ecological data used in this study is accessible online through www.reeflifesurvey.com. Correspondence and requests for other materials should be addressed to rstuarts@utas.edu.au.

## References

1 Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. & Langham, G. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**, e325, doi:10.1371/journal.pbio.0060325 (2008).

2 Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C. & Mace, G. M. Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**, 53-58, doi:10.1126/science.1200303 (2011).

3 Watson, J. E. M., Iwamura, T. & Butt, N. Mapping vulnerability and conservation adaptation strategies under climate change. *Nature Clim. Change* **3**, 989-994, doi:10.1038/nclimate2007 (2013).

4 Burrows, M. T. *et al.* Geographical limits to species-range shifts are suggested by climate velocity. *Nature* **507**, 492-495, doi:10.1038/nature12976 (2014).

5 Burrows, M. T. *et al.* The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652-655, doi:10.1126/science.1210288 (2011).

6 García Molinos, J. *et al.* Climate velocity and the future global redistribution of marine biodiversity. *Nature Clim. Change* **advance online publication**, doi:10.1038/nclimate2769 (2015).

7 Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E. & Kirby, R. R. Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nature Clim. Change* **5**, 695-701, doi:10.1038/nclimate2650 (2015).

8 Lima, F. P. & Wethey, D. S. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nat Commun* **3**, 704, doi:http://www.nature.com/ncomms/journal/v3/n2/suppinfo/ncomms1713_S1.html (2012).

9 Foden, W. B. *et al.* Identifying the World's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* **8**, e65427, doi:10.1371/journal.pone.0065427 (2013).

10 Pacifici, M. *et al.* Assessing species vulnerability to climate change. *Nature Clim. Change* **5**, 215-224, doi:10.1038/nclimate2448 (2015).

11 Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences* **278**, 1823-1830, doi:10.1098/rspb.2010.1295 (2011).

12 Sunday, J. M. *et al.* Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.*, n/a-n/a, doi:10.1111/ele.12474 (2015).

13 Kordas, R. L., Harley, C. D. G. & O'Connor, M. I. Community ecology in a warming world: The influence of temperature on interspecific interactions in marine systems. *J. Exp. Mar. Biol. Ecol.* **400**, 218-226, doi:http://dx.doi.org/10.1016/j.jembe.2011.02.029 (2011).

14 Okey, T. A., Agbayani, S. & Alidina, H. M. Mapping ecological vulnerability to recent climate change in Canada's Pacific marine ecosystems. *Ocean Coast. Manage.* **106**, 35-48, doi:http://dx.doi.org/10.1016/j.ocecoaman.2015.01.009 (2015).

15 Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences* **275**, 2743-2748, doi:10.1098/rspb.2008.0878 (2008).

16 Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Clim. Change* **2**, 121-124, doi:http://www.nature.com/nclimate/journal/v2/n2/abs/nclimate1347 (2012).

17 Zografou, K. *et al.* Signals of Climate Change in Butterfly Communities in a Mediterranean Protected Area. *PLoS ONE* **9**, e87245, doi:10.1371/journal.pone.0087245 (2014).

18 Bates, A. E. *et al.* Resilience and signatures of tropicalization in protected reef fish communities. *Nature Climate Change* **4**, 62-67, doi:10.1038/nclimate2062 (2014).

19 Cheung, W. W. L., Watson, R. & Pauly, D. Signature of ocean warming in global fisheries catch. *Nature* **497**, 365-368 (2013).

20 Edgar, G. J. & Stuart-Smith, R. D. Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data* **1**, 140007, doi:10.1038/sdata.2014.7 (2014).

21 Edgar, G. J. & Stuart-Smith, R. D. Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Mar. Ecol. Prog. Ser.* **388**, 51-62 (2009).

22 Tyberghein, L. *et al.* Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecol. Biogeogr.* **21**, 272-281, doi:10.1111/j.1466-8238.2011.00656.x (2012).

23 Tittensor, D. P. *et al.* Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098-1101 (2010).

24 Stuart-Smith, R. D. *et al.* Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* **501**, 539-542, doi:10.1038/nature12529 (2013).

25 Magnuson, J. J., Crowder, L. B. & Medvick, P. A. Temperature as an ecological resource. *Am. Zool.* **19**, 331-343, doi:10.1093/icb/19.1.331 (1979).

26 Jablonski, D. *et al.* Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 10487-10494, doi:10.1073/pnas.1308997110 (2013).

27 Kellermann, V. *et al.* Upper thermal limits of Drosophila are linked to species distributions and strongly constrained phylogenetically. *Proc Natl Acad Sci U S A* **109**, 16228-16233, doi:10.1073/pnas.1207553109 (2012).

28 Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427**, 145-148 (2004).

29 Mumby, P. J., Chollett, I., Bozec, Y.-M. & Wolff, N. H. Ecological resilience, robustness and vulnerability: how do these concepts benefit ecosystem management? *Current Opinion in*

*Environmental Sustainability* **7**, 22-27, doi:http://dx.doi.org/10.1016/j.cosust.2013.11.021 (2014).

30 Reynolds, R. W., Rayner, N. A., Smith, T. M., Stokes, D. C. & Wang, W. An Improved In Situ and Satellite SST Analysis for Climate. *J. Clim.* **15**, 1609-1625, doi:10.1175/1520-0442(2002)015<1609:AIISAS>2.0.CO;2 (2002).

31 Hiddink, J. G. & Ter Hofstede, R. Climate induced increases in species richness of marine fishes. *Global Change Biology* **14**, 453-460, doi:10.1111/j.1365-2486.2007.01518.x (2008).

32 Nguyen, K. D. T. *et al.* Upper Temperature Limits of Tropical Marine Ectotherms: Global Warming Implications. *PLoS ONE* **6**, e29340, doi:10.1371/journal.pone.0029340 (2011).

33 Pörtner, H. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* **88**, 137-146, doi:10.1007/s001140100216 (2001).

34 Pörtner, H. O. & Knust, R. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95-97, doi:10.1126/science.1135471 (2007).

35 Figueira, W. F., Biro, P., Booth, D. J. & Valenzuela, V. C. Performance of tropical fish recruiting to temperate habitats: Role of ambient temperature and implications of climate change. *Mar. Ecol. Prog. Ser.* **384**, 231-239 (2009).

36 Brown, J. H., Stevens, G. C. & Kaufman, D. M. The Geographic Range: Size, Shape, Boundaries, and Internal Structure. *Annu. Rev. Ecol. Syst.* **27**, 597-623, doi:10.2307/2097247 (1996).

37 Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nature Clim. Change* **2**, 686-690, doi:http://www.nature.com/nclimate/journal/v2/n9/abs/nclimate1539.html#supplementary-information (2012).

38 Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O. & Huey, R. B. Climate change tightens a metabolic constraint on marine habitats. *Science* **348**, 1132-1135, doi:10.1126/science.aaa1605 (2015).

39 Graham, N. A. J. *et al.* Dynamic fragility of oceanic coral reef ecosystems. *Proc. Natl. Acad. Sci. USA* **103**, 8425-8429 (2006).

40 Araújo, M. B. *et al.* Heat freezes niche evolution. *Ecol. Lett.* **16**, 1206-1219, doi:10.1111/ele.12155 (2013).

41 Tilman, D. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81-92 (1997).

42 Victor, D. G. & Kennel, C. F. Climate policy: Ditch the 2 °C warming goal. *Nature* **514**, 30-31 (2014).

43 Spalding, M. D. *et al.* Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* **57**, 573-583 (2007).

44 Bates, A. E. *et al.* Distinguishing geographical range shifts from artefacts of detectability and sampling effort. *Divers. Distrib.*, n/a-n/a, doi:10.1111/ddi.12263 (2014).

## Figure legends

**Figure 1. Global community temperature index (CTI) for reef fishes (a) and invertebrates (b) against mean annual sea surface temperature (SST).** Tropical and temperate communities are separated by sub-tropical transitions in which communities largely comprise a mixture of temperate and tropical species. A line with a slope of one is plotted for reference. N = 2,175 & 1,901 sites for fishes and invertebrates, respectively, after exclusion of sites with confidence scores <2.5 (see methods).

**Figure 2. Frequency distributions of fish (a) and invertebrate (b) species according to their thermal distribution midpoint show modes of temperature affinity, or tropical (red), temperate (blue) and subpolar (white) thermal guilds**. Species for which confidence in thermal midpoints was low are excluded (see methods).

**Figure 3. Vulnerability of marine communities to warming-related local species loss.** Proportion of fish and invertebrate species in present-day communities likely to exceed their upper realised thermal limit by 2025 (a) and 2115 (c) based on regional IPCC warming rates (RCP8.5 scenario), and in relation to the magnitude of community thermal bias (measured as $\text{TBias}_{\text{max}}$; b, d). Fitted curves (solid black line) and 95% confidence intervals (dotted black lines) are from GAMM models (Extended Data Table 2). Sites with confidence scores <2.5 were excluded from most ecoregion[43] means (See ED Table 1 for sample sizes and details of exclusions).

## Methods

### Reef fish and invertebrate data

Standardised quantitative censuses of reef fishes and echinoderms (holothurians, echinoids, asteroids, crinoids), molluscs (gastropods, cephalopods), and crustaceans (decapods) were undertaken by trained recreational SCUBA divers along 7,040 transects at 2,447 sites worldwide through the Reef Life Survey (RLS) program. Full details of fish census methods are provided in[20,21], and an online methods manual ([www.reeflifesurvey.com](www.reeflifesurvey.com)) describes all data collection methods, including for invertebrates. Data quality and training of divers are detailed in[20] and supplementary material in[24]. Data used in this study are densities of all species recorded per 500 m$^2$ transect area for fishes (2 x 250 m$^2$ blocks), and per 100 m$^2$ for invertebrates (2 x 50 m$^2$ blocks). Four percent of all records were not identified to species level (mostly invertebrates) and were omitted from analyses for this study.

Data from fish and invertebrate surveys were analysed separately for thermal biogeography analyses, but combined for the vulnerability predictions shown in Fig 3. Although collected on the same transect lines, these survey components were collected over different areal extents, and so were combined to represent densities per 50 m$^2$ (block size for invertebrate surveys). Raw invertebrate data were therefore used, but one in five individual fishes were randomly subsampled from those surveyed in each 250 m$^2$ block to provide equivalent densities and richness of fishes per 50 m$^2$.

### Characterisation of species' thermal distributions

A realised thermal distribution was constructed for all species recorded on RLS transects, based on occurrences rather than species distribution models. All individual records within the RLS database were combined with all records of these species in the Global Biodiversity Information Facility (GBIF: http://www.gbif.org/), after applying filters to limit records to depths shallower than 26m and time of collection since 2004. This resulted in a dataset of 399,927 geo-referenced occurrences of 3,920 species.

Remotely sensed local sea surface temperature (SST) data were then matched to each occurrence location. Long-term mean annual SST values from 2002-2009 from the Bio-Oracle dataset[22] were used to provide a time-integrated picture of temperatures species were typically associated with for the thermal biogeographic analysis. The 5th and 95th percentiles of the temperature distribution occupied by each species were then calculated, and the midpoint between these used as a measure of central tendency of their realised thermal distribution. Midpoints were considered a reasonable proxy for the temperature associated with species' maximum ecological success, confirmed by a close alignment of midpoints with the temperatures at which species occurred in maximum abundance in the global RLS dataset (slope of midpoint vs temperature of sites at which species were at maximum abundance = 1.003, Pearson correlation = 0.93, $P<0.001$). Thus, inter-specific variation is expected, deviation in temperatures either side of the midpoint results in reduced abundance for the average species.

We also calculated and explored other metrics from the thermal range, including the median and mode, but these were more sensitive to the distribution and intensity of sampling effort across the temperature range of species, and therefore less robust than the midpoints. Fifth and 95th percentiles were deliberately chosen as endpoints rather than the maximum and minimum because marine species range boundaries are not static, with dynamic tails in distributions[44]. Sightings of individual vagrants are common, sometimes at large distances from the nearest viable populations.

Furthermore, any misidentification errors would have greatest influence if at the edge of species ranges.

### Community Temperature Index (CTI) calculation and thermal bias

CTI was calculated separately for fishes and invertebrates for each transect in the RLS database as the average of thermal midpoint values for each species recorded, weighted by their log(X+1) abundance. Multiple transects were usually surveyed at each site (2.8 transects global mean across sites used in this study). CTI values were averaged across these to create a site-level mean that was used for analyses. In some cases this averaged out seasonal effects, where sites were surveyed across multiple seasons.

Thermal bias was calculated as the difference between the CTI and mean annual SST at each site. Mean thermal bias values across sites surveyed in each ecoregion are shown in ED Fig 3, with sample sizes for ecoregions shown in ED Table 1.

### Confidence scores

The number of occurrence records for each species ranged from a single record (numerous species) to 1,009 (the Indo-Pacific cleaner wrasse, *Labroides dimidiatus*), with an overall mean of 36 records (47 for fishes, 16 for invertebrates). In order to consider how variation in the comprehensiveness of data on the thermal distribution for each species affected the calculation of CTI and provide an objective measure of confidence in site-level CTI values, we used a semi-quantitative confidence scoring system. A confidence value ranging from one (very little confidence) to three (high confidence) was allocated to each species through a four step process:

(1) The number of records (sites) for each species was used as a first pass for classification, with species observed at 30 or more sites given a value of three, 10-29 sites a value of two, and less than 10 sites a value of one.

(2) The thermal range for each species (the difference between 95th and 5th percentiles) was used in a second pass for all species that were initially given a value of two. For this, those species with a thermal range of less than 3°C were reduced to a value of one, as it is possible these species have not been surveyed across their full potential thermal range.

(3) Species with a value of three and a thermal range of less than 1°C were reduced to a two, given these likely represent well-sampled, but range-restricted species, and their potential thermal range is likely greater than their realised range (which is likely limited by other factors such as dispersal or historical biogeography).

(4) The frequency of occurrences across temperatures was also plotted separately for each species. Frequency histograms were visually inspected as a last pass, and confidence scores reduced by one if the thermal distribution appeared to be unduly influenced by widely separated records.

We then recalculated CTI for using confidence scores for each species, weighted by their abundance (also log(X+1) transformed), creating a CTI confidence score for each transect and each site. A mean site confidence score of >2.5 was used as a cut-off for many analyses and figures, as indicated in figure captions. Although a score of 2.5 can be achieved in many ways, this effectively represents at least 75% of the individuals present belonging to species with the maximum confidence score of three.

### Thermal guilds

Given few truly subtropical species were identified in this study, and this outcome could potentially result from bias in the distribution of sampling effort towards areas outside of subtropical locations (see Supplementary Information for more detail), we replicated Figure 2 along a comprehensively-sampled latitudinal gradient in Australia. The majority of Australian species are well-sampled across their geographic distributions and numerous sites have been surveyed in subtropical locations in Australia. We divided the RLS data from 968 sites into 10° latitudinal bands along the east coast of Australia (and Papua New Guinea and Solomon Islands) from the equator to 43.7°S, and plotted histograms of thermal distribution midpoints of 1,105 species with a confidence of two or three (ED Fig 6). These clearly show very few species with midpoints of 23-24°C, even in the band from 20°S-30°S where the mean annual SST of sites was 23.97°C. They also show the intrusion of numerous tropical species in temperate latitudes, particularly for fishes.

## Vulnerability predictions

Vulnerability predictions required characterisation of the warmest temperatures experienced by species across their range. We re-constructed the thermal distributions for each species using maximum of the weekly mean SST from all occurrence sites over the 12 weeks prior to the sampling date, obtaining the 95th percentile of these. We then calculated the difference between this value and the mean of summer temperatures (the mean of the warmest 8 weeks was taken for each year between 2008 and 2014, with the mean of these used). This is analogous to a form of thermal safety margin, although in this case it does not mean a species cannot survive if the summer SST exceeds the 95th percentile, but rather that it has been recorded at very few sites in the combined RLS and GBIF databases at times in which the temperatures exceeded this value.

We re-calculated this value for 10 years and 100 years from present, using rates of SST warming projected by coupled climate models' CMIP5 PCP8.5 scenario, calculated and freely provided by the

NOAA Ocean Climate Change Web Portal (http://www.esrl.noaa.gov/psd/ipcc/ocn/). Sea surface temperature anomaly (difference in the mean climate in the future time period, 2050-2099, compared to the historical reference period, 1956-2005) was selected as the statistic representing the average of 25 models, interpolated to a 1° latitude by 1° longitude grid and matched to each RLS site. Summer SST was predicted for each RLS site for 10 and 100 year time periods using these values. Vulnerability was then estimated as the proportion of all species (fishes and invertebrates) recorded on each RLS survey that is expected to exceed the 95th percentile, based on the predicted SST at that site. This component of analyses did not incorporate abundance data, as the goal was to assess local species loss, rather than loss of individuals. Weighting by abundance had little influence on conclusions, however.

Confidence scores were also recalculated without abundance (and thus represent the mean confidence of species present), and sites with confidence scores <2.5 were excluded from calculation of ecoregion means for all ecoregions with three or more sites with confidence >2.5. Twenty-one of 81 ecoregions had fewer than three sites with confidence >2.5 with which to calculate means, so low confidence sites were included in means for these ecoregions. The effect of this is conservative, theoretically reducing thermal bias (see Supplementary Information), but the rationale was that ecoregion means would be more accurate through their inclusion than if heavily weighted by few sites. To provide an additional cut-off for ecoregions in which the overall mean confidence was still low, we excluded ecoregions with mean confidence <1.75. This resulted in the exclusion of six ecoregions (North and East Barents Sea, Oyashio Current, Agulhas Bank, Sea of Japan/East Sea, Gulf of Maine/Bay of Fundy, Malvinas/Falklands).

To explore the contributions of warming rates and thermal bias to vulnerability predictions, we also recalculated CTI as the mean 95th percentiles of fish and invertebrate species recorded on transects ($CTI_{max}$) and thermal bias ($TBias_{max}$) as the difference between site-level $CTI_{max}$ and mean summer SST. $TBias_{max}$ can therefore be considered the sensitivity component of the vulnerability predictions, based on recent mean summer SST and not accounting for warming rates (exposure). We applied GAMMs to assess vulnerability scores as a function of $TBias_{max}$ and warming rates, with ecoregion as a random factor (ED Table 2).

Conclusions are robust to the warming data used, with qualitatively similar results using historical warming data from another source[8], instead of future predictions (site warming rates in °C per decade taken from [http://www.coastalwarming.com/data.html](http://www.coastalwarming.com/data.html)), and ecoregion mean vulnerability scores changing very little when the 99th percentile of species' thermal distributions were used instead of the 95th percentile, even for 2115 predictions (Pearson correlation =0.97, P<0.01).

## Extended Data legends

**Extended Data Figure 1. Sites used in analyses at which fish and invertebrate communities were surveyed by the Reef Life Survey program.** Numerous points are overlapping and hidden (n = 2,447). Ecoregion boundaries are shown in grey lines.

**Extended Data Figure 2. Community Temperature Index (CTI) of reef fishes and invertebrates against mean annual sea surface temperature (SST)**. CTI calculated using abundance-weighted fish (a) and invertebrate (b) data, and including sites at which mean CTI confidence scores were less than 2.5 (N= 2,447 and 2,383 for fishes and invertebrates, respectively). Sites are colour-coded by ecoregion to help distinguish spatial patterns, but as a result of numerous ecoregions (N=81), many ecoregion colours are similar. CTI calculated using presence-only fish (c) and invertebrate (d) data, and excluding sites with confidence scores <2.5 (N=2,188 and 1,812 for fishes and invertebrates, respectively). Dotted lines have a slope of one, plotted for comparison with data.

**Extended Data Figure 3. Global distribution of reef fish (a) and invertebrate (b) community thermal bias.** Community thermal bias ($^{o}$C) is the difference in abundance-weighted Community Temperature Index (CTI) from local long-term mean annual sea surface temperature. Positive regions (warm colours) encompass ecological communities with a predominance of individuals with warmer thermal affinity than mean local sea temperatures. Colours are scaled to the mean thermal bias of sites surveyed within each ecoregion (see Extended Data Table 1 for sample sizes). Only ecoregions with sites surveyed are included.

**Extended Data Figure 4. Frequency distribution of fish (a) and invertebrate (b) species' latitudinal range midpoints.** Species for which confidence in thermal distribution midpoints (and therefore geographical distribution midpoints) was low are excluded (see methods).

**Extended Data Figure 5. Frequency distribution of fish (left) and invertebrate (right) species' thermal distribution midpoints in 10$^{o}$ latitudinal bands from Papua New Guinea down eastern Australia (rows).** Note Y-axes are on different scales and only species with confidence scores of two and three are included (see methods).

**Extended Data Figure 6. Frequency distribution of thermal distribution midpoints of species in major fish families spanning temperate and tropical zones.** Note Y-axes are on different scales and only species with confidence scores of two and three are included.

**Extended Data Figure 7. Global distribution of $TBias_{max}$ of reef faunal communities.** $TBias_{max}$ is calculated as the difference between $CTI_{max}$ (using the 95th percentiles of species' thermal distributions and presence data) and mean summer SST. Colours are scaled to the mean $TBias_{max}$ of sites surveyed within each ecoregion (see Extended Data Table 1 for sample sizes). Only ecoregions in which quantitative surveys were undertaken are included.

**Extended Data Figure 8. The $CTI_{max}$ (mean 95th percentile of species thermal distributions) for reef faunal communities across temperate (blue), tropical (red) and subtropical (grey) sites.** SST data are means of the warmest eight weeks of the year over the survey period (2008-2014). Points represent the surveyed community of fishes and invertebrates at each site (N=2,091, only confidence scores >2.5). Regression lines are fitted to the maximum values within each ecoregion, with separate regressions fitted for sites categorised from Figure 1 as temperate, tropical and subtropical.

**Extended Data Table 1. Ecoregion means, sample sizes and vulnerability predictions.** The number of sites used in figures is the number of sites with confidence > 2.5, with number of sites with confidence <2.5 shown in brackets. An asterisk indicates that sites with confidence <2.5 were included in calculations of ecoregion means. Group identifies whether fauna surveyed at sites within the ecoregion can be classified as temperate (TE), tropical (TR), sub-tropical (ST), sub-polar (SP), and temperate-subpolar transition (TE-SP) on the basis of CTI.

**Extended Data Table 2. GAMM results for Figure 3b and d**. Proportion of species loss predicted by 2025 and 2115 as a function of warming rate and $\mathrm{TBias}_{\mathrm{max}}$. N=2,091