

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

2 R.D. Stuart-Smith*¹, G.J. Edgar¹, N.S. Barrett¹, S.J. Kininmonth², A.E. Bates³

4 ¹Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, 7001 Australia

²Stockholm Resilience Centre, Stockholm University, Kräftriket Stockholm, 2B, SE-106 91 Sweden

6 ³Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton,
Southampton, SO14 3ZH UK

8

Summary

10 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
12 average, approximate local environmental temperatures. Nevertheless, we find most shallow water
marine species occupy broad thermal distributions that are aggregated in either temperate or
14 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
16 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-
18 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
20 present-day species' distributional ranges, outweighs spatial variation in warming rates in
contributing to predicted rates of local species loss.

22

Main text

24 The inherent vulnerability of ecological communities to global warming, and therefore the
26 magnitude of associated biodiversity change, is considered a function of exposure and sensitivity to
warming, coupled with species' adaptive capacity¹⁻³. Geographic models of future biodiversity
change generally accommodate the magnitude, direction and distribution of temperature change⁴⁻⁸,
28 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
30 life-history traits, often with extension from the laboratory to the field⁹⁻¹². Extrapolation to whole
ecological communities and large geographic scales, does, however, introduce substantial
32 uncertainty, yet these are the scales critical for understanding natural ecosystem functioning¹³, on
which the well-being of human society depends.

34 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
36 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
38 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
40 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
42 sensitivity to negative change with warming. In this case, proxies previously used for inferring
sensitivity, such as habitat type or integrity³, may provide limited predictive insight. Quantifying the
44 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
46 warming, and providing a more direct means to account for sensitivity in predictions of vulnerability.

48 Thermal Biogeography

50 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}, butterflies¹⁷ and fishes¹⁸, and global commercial fisheries catches¹⁹. 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.

54 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 temperature²². 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.

62 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.

66 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

72 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
74 cooler affinity than the local environment.

The proximate cause of large-scale patterns of thermal bias is that marine species distributions do
76 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
78 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
80 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).

82 Thermal guilds align with the theory that temperature can be considered as an ecological resource in
freshwater fishes²⁵, and can be distinguished within other independent datasets of marine species
84 (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
86 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
88 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
90 continental shelf area at subtropical latitudes globally²⁶; (b) Historical biogeographic processes could
be implied for the Australian fauna, through mixing of tropical Pacific/south-east Asian and
92 temperate Australian faunas as the Australian continental plate drifted north, with species
conserving thermal preferences (i.e. phylogenetic inertia²⁷); (c) Tropical centres of speciation and
94 subsequent colonisation of temperate regions through 'bridge species' may have occurred (the 'out
of the tropics' hypothesis²⁶), and is supported by the distributions of thermal affinities of species in
96 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-
98 offs in metabolic processes reducing widespread adaptation to intermediate temperatures.

Regardless of the ultimate drivers, the existence of consistent thermal guilds and associated global-
100 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
102 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
104 of the species present.

106 **Vulnerability of marine communities to warming**

Most previous biodiversity vulnerability analyses have focussed on species, and their ability to
108 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-
110 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
112 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
114 management goals of resilience or stability in the face of warming²⁹.

Over decadal scales, positive thermal bias of the magnitude observed for some locations in this
116 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
118 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
120 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
122 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
124 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
126 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
128 predatory environment.

For calculation of CTI_{max} to estimate species loss with warming, we used presence rather than
130 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-
132 calculated thermal bias (TBias_{max}) as the difference between CTI_{max} and mean summer temperatures
(mean SST from the 8 warmest weeks annually from 2008-2014³⁰). This can be considered a form of
134 '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;
136 n = 2,089; p<0.01).

CTI_{max} also shows a stepped relationship with summer SST (ED Fig 8), reflecting some consistencies
138 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
140 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
142 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)
144 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.

146 While $T_{Bias_{max}}$ 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
148 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
150 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
152 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
154 sea surface temperature anomaly under the RCP8.5 scenario predicted for 2050-2099;
<http://www.esrl.noaa.gov/psd/ipcc/>).

156 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
158 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
160 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
162 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
164 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
166 instead correspond closely to the magnitude of thermal bias (measured as $T_{Bias_{max}}$; Fig 3 b, d;
GAMM results in ED Table 2). This result is robust to the warming data used (See Supplementary
168 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
170 rate predictions, may be considerably less important than previously suggested¹ when it comes to

172 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
174 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
176 summer SST (mean $T_{Bias_{max}} = 6.3^{\circ}C \pm 1.1SD$).

Our predictions do not account for local influx of warmer affinity species, and do not comprise the
178 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
180 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
182 Australia¹². 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
184 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
186 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
188 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
190 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,
192 especially narrow range endemics which are probably limited in distribution by factors other than
temperature¹². Regardless, we consider this generalisation reasonable in light of the well-connected
194 nature of the marine environment, typically large geographic ranges³⁶, and often closely matching
fundamental (assessed in laboratory experiments) and realised (field-derived from distribution data)

196 thermal niches³⁷, as well as implications associated with lower concentrations of dissolved oxygen in
the marine environment with increasing temperature³⁸.

198 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
200 particularly true for indirect effects of extreme events, such as through habitat change, which place
critical pressures on biodiversity³⁹, and represent an important direction for future research.

202 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
204 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
206 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
208 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
210 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,
212 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
214 fundamental element affecting global variability in future biodiversity change.

216 **Tracking and managing warming impacts on marine biodiversity**

In contrast to prior global studies of potential biodiversity losses associated with climate change,
218 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

220 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
222 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.

224 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
226 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
228 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
230 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;
232 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
234 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
236 reduce influx of warm affinity species at those regions where accumulation is predicted. Actions to
support more intact naturally-functioning communities are recommended, including
238 implementation of marine protected areas (MPAs) and more conservative fisheries management.
Recent evidence from an effective temperate MPA suggests that local predators hinder poleward
240 progression of warm-affinity species¹⁸, and invasion theory more generally predicts intact and
diverse natural communities possess greater resistance to invasive species than degraded
242 communities⁴¹.

Abundance-weighted CTI, as used in our thermal biogeographic analysis, offers an important tool for
244 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 scales¹⁵, 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 CO₂ concentrations and ocean heat content⁴², 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.

Acknowledgements

We thank the many Reef Life Survey (RLS) divers who participated in data collection and provide ongoing expertise and commitment to the program, University of Tasmania staff including Just Berkhout, Antonia Cooper, Marlene Davey, Justin Hulls, Elizabeth Oh, Jemina Stuart-Smith and Russell Thomson. Development of RLS was supported by the former Commonwealth Environment Research Facilities Program, while analyses were supported by the Australian Research Council, Institute for Marine and Antarctic Studies, and the Marine Biodiversity Hub, a collaborative partnership supported through the Australian Government's National Environmental Science Programme. Additional funding and support for field surveys was provided by grants from the Ian Potter Foundation, CoastWest, National Geographic Society, Conservation International, Wildlife Conservation Society Indonesia, The Winston Churchill Memorial Trust, Australian-American Fulbright Commission, and ASSEMBLE Marine. The comments of anonymous reviewers were also appreciated.

270 **Author contributions**

RDSS, AEB and GJE conceived the idea, GJE, RDSS and many others collected the data. RDSS drafted
272 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
274 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.
276 Correspondence and requests for other materials should be addressed to rstuarts@utas.edu.au.

278 **References**

- 1 Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. & Langham, G. Towards an integrated
280 framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**, e325,
doi:10.1371/journal.pbio.0060325 (2008).
- 282 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,
284 doi:10.1126/science.1200303 (2011).
- 3 Watson, J. E. M., Iwamura, T. & Butt, N. Mapping vulnerability and conservation adaptation
286 strategies under climate change. *Nature Clim. Change* **3**, 989-994, doi:10.1038/nclimate2007
(2013).
- 288 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).
- 290 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).
- 292 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
294 (2015).
- 7 Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E. & Kirby, R. R. Future vulnerability of
296 marine biodiversity compared with contemporary and past changes. *Nature Clim. Change* **5**,
695-701, doi:10.1038/nclimate2650 (2015).
- 298 8 Lima, F. P. & Wethey, D. S. Three decades of high-resolution coastal sea surface
300 temperatures reveal more than warming. *Nat Commun* **3**, 704,
doi:http://www.nature.com/ncomms/journal/v3/n2/supinfo/ncomms1713_S1.html
(2012).

302 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,
 304 doi:10.1371/journal.pone.0065427 (2013).

10 Pacifici, M. *et al.* Assessing species vulnerability to climate change. *Nature Clim. Change* **5**,
 306 215-224, doi:10.1038/nclimate2448 (2015).

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

310 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).

312 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.*
 314 *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
 316 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).

318 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,
 320 doi:10.1098/rspb.2008.0878 (2008).

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

324 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).

326 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).

328 19 Cheung, W. W. L., Watson, R. & Pauly, D. Signature of ocean warming in global fisheries
 catch. *Nature* **497**, 365-368 (2013).

330 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).

332 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).

334 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-
 336 8238.2011.00656.x (2012).

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

24 Stuart-Smith, R. D. *et al.* Integrating abundance and functional traits reveals new global
 340 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.*
 342 *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
 344 the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National*
Academy of Sciences of the United States of America **110**, 10487-10494,
 346 doi:10.1073/pnas.1308997110 (2013).

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

350 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
 352 vulnerability: how do these concepts benefit ecosystem management? *Current Opinion in*

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

356 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).

358 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).

360 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).

362 33 Pörtner, H. Climate change and temperature-dependent biogeography: oxygen limitation of
 thermal tolerance in animals. *Naturwissenschaften* **88**, 137-146,
 364 doi:10.1007/s001140100216 (2001).

366 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).

368 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).

370 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
 372 (1996).

374 37 Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of
 animals. *Nature Clim. Change* **2**, 686-690,
 376 doi:http://www.nature.com/nclimate/journal/v2/n9/abs/nclimate1539.html#supplementar
 y-information (2012).

378 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).

380 39 Graham, N. A. J. *et al.* Dynamic fragility of oceanic coral reef ecosystems. *Proc. Natl. Acad.*
Sci. USA **103**, 8425-8429 (2006).

382 40 Araújo, M. B. *et al.* Heat freezes niche evolution. *Ecol. Lett.* **16**, 1206-1219,
 doi:10.1111/ele.12155 (2013).

384 41 Tilman, D. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*
78, 81-92 (1997).

386 42 Victor, D. G. & Kennel, C. F. Climate policy: Ditch the 2 °C warming goal. *Nature* **514**, 30-31
 (2014).

388 43 Spalding, M. D. *et al.* Marine ecoregions of the world: a bioregionalization of coastal and
 shelf areas. *Bioscience* **57**, 573-583 (2007).

390 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).

394

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 $T_{Bias_{max}}$; 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 ecoregion⁴³ means (See ED Table 1 for sample sizes and details of exclusions).

Methods

420 Reef fish and invertebrate data

Standardised quantitative censuses of reef fishes and echinoderms (holothurians, echinoids,
422 asteroids, crinoids), molluscs (gastropods, cephalopods), and crustaceans (decapods) were
undertaken by trained recreational SCUBA divers along 7,040 transects at 2,447 sites worldwide
424 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) describes all data collection methods,
426 including for invertebrates. Data quality and training of divers are detailed in²⁰ and supplementary
material in²⁴. Data used in this study are densities of all species recorded per 500 m² transect area
428 for fishes (2 x 250 m² blocks), and per 100 m² for invertebrates (2 x 50 m² blocks). Four percent of all
records were not identified to species level (mostly invertebrates) and were omitted from analyses
430 for this study.

Data from fish and invertebrate surveys were analysed separately for thermal biogeography
432 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
434 were combined to represent densities per 50 m² (block size for invertebrate surveys). Raw
invertebrate data were therefore used, but one in five individual fishes were randomly subsampled
436 from those surveyed in each 250 m² block to provide equivalent densities and richness of fishes per
50 m².

438

Characterisation of species' thermal distributions

440 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
442 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
444 of collection since 2004. This resulted in a dataset of 399,927 geo-referenced occurrences of 3,920
species.

446 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 dataset²² were
448 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
450 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
452 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
454 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
456 variation is expected, deviation in temperatures either side of the midpoint results in reduced
abundance for the average species.

458 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
460 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
462 marine species range boundaries are not static, with dynamic tails in distributions⁴⁴. Sightings of
individual vagrants are common, sometimes at large distances from the nearest viable populations.

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

466

Community Temperature Index (CTI) calculation and thermal bias

468 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 $\log(X+1)$
470 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
472 used for analyses. In some cases this averaged out seasonal effects, where sites were surveyed
across multiple seasons.

474 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
476 sizes for ecoregions shown in ED Table 1.

478 Confidence scores

The number of occurrence records for each species ranged from a single record (numerous species)
480 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
482 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
484 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:

486 (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
488 less than 10 sites a value of one.

(2) The thermal range for each species (the difference between 95th and 5th percentiles) was
490 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
492 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,
494 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
496 factors such as dispersal or historical biogeography).

(4) The frequency of occurrences across temperatures was also plotted separately for each
498 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
500 separated records.

We then recalculated CTI for using confidence scores for each species, weighted by their abundance
502 (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
504 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
506 three.

508 **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.

520

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

532

NOAA Ocean Climate Change Web Portal (<http://www.esrl.noaa.gov/psd/ipcc/ocn/>). Sea surface
534 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
536 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
538 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
540 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
542 on conclusions, however.

Confidence scores were also recalculated without abundance (and thus represent the mean
544 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
546 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,
548 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
550 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
552 ecoregions (North and East Barents Sea, Oyashio Current, Agulhas Bank, Sea of Japan/East Sea, Gulf
of Maine/Bay of Fundy, Malvinas/Falklands).

554 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
556 (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,

558 based on recent mean summer SST and not accounting for warming rates (exposure). We applied
GAMMs to assess vulnerability scores as a function of $T_{Bias_{max}}$ and warming rates, with ecoregion as
560 a random factor (ED Table 2).

Conclusions are robust to the warming data used, with qualitatively similar results using historical
562 warming data from another source⁸, instead of future predictions (site warming rates in °C per
decade taken from <http://www.coastalwarming.com/data.html>), and ecoregion mean vulnerability
564 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).

566

568 **Extended Data legends**

570 **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 =
572 2,447). Ecoregion boundaries are shown in grey lines.

574 **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
576 (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
578 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,

580 and excluding sites with confidence scores <2.5 ($N=2,188$ and $1,812$ for fishes and invertebrates,
581 respectively). Dotted lines have a slope of one, plotted for comparison with data.

582

Extended Data Figure 3. Global distribution of reef fish (a) and invertebrate (b) community

584 **thermal bias.** Community thermal bias ($^{\circ}\text{C}$) is the difference in abundance-weighted Community
Temperature Index (CTI) from local long-term mean annual sea surface temperature. Positive
586 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
588 bias of sites surveyed within each ecoregion (see Extended Data Table 1 for sample sizes). Only
ecoregions with sites surveyed are included.

590

Extended Data Figure 4. Frequency distribution of fish (a) and invertebrate (b) species' latitudinal

592 **range midpoints.** Species for which confidence in thermal distribution midpoints (and therefore
geographical distribution midpoints) was low are excluded (see methods).

594

Extended Data Figure 5. Frequency distribution of fish (left) and invertebrate (right) species'

596 **thermal distribution midpoints in 10° 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
598 and three are included (see methods).

600 **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
602 only species with confidence scores of two and three are included.

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

610 **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
612 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
614 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
616 subtropical.

618 **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
620 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

622 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.

624

Extended Data Table 2. GAMM results for Figure 3b and d. Proportion of species loss predicted by

626 2025 and 2115 as a function of warming rate and $T_{Bias_{max}}$. N=2,091

Post-print