



Most 'global' reviews of species' responses to climate change are not truly global

Kenneth J. Feeley^{1,2*}, James T. Stroud^{1,2} and Timothy M. Perez^{1,2}

¹International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA, ²Fairchild Tropical Botanic Garden, Coral Gables, FL 33156, USA

ABSTRACT

It is critical that we understand the effects of climate change on natural systems if we ever hope to predict or mitigate consequent changes in diversity and ecosystem function. In order to identify coherent 'fingerprints' of climate change across Earth's terrestrial and marine ecosystems, various reviews have been conducted to synthesize studies of climate change impacts on individual species, assemblages and systems. These reviews help to make information about climate change impacts accessible for researchers as well as for the general public and policymakers. As such, these reviews can be highly influential in setting the direction of policy and research. Unfortunately, due to limited data availability, the majority of reviews of climate change impacts suffer from severe taxonomic and geographic biases. In particular, tropical and marine systems are grossly underrepresented, as are plants and endothermic animals. These biases may preclude a comprehensive understanding of how climate change is affecting Earth's natural systems at a global scale. In order to advance our understanding of climate change impacts on species and ecosystems, we need to first assess the types of data that are and are not available and then correct these biases through directed studies and initiatives.

Keywords

climate change, climate change responses, geographic bias, global review, marine, taxonomic bias, terrestrial.

*Correspondence: Kenneth J. Feeley, Department of Biology, The University of Miami, Coral Gables, FL 33146, USA. E-mail: kjfeeley@gmail.com

Anthropogenic climate change is a truly global phenomenon that has the potential to impact all species in all ecosystems. In order to gain a better understanding of the possible impacts of climate change, various studies have examined the responses of individual species or ecosystems to changes in climate through time. These studies have in turn been synthesized into a number of different reviews that attempt to identify 'globally coherent fingerprints' of climate change (e.g. Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006; Chen *et al.*, 2011; Poloczanska *et al.* 2013; Lenoir & Svenning, 2015; Pearce-Higgins *et al.*, 2015; Brown *et al.*, 2016). These reviews are highly cited – often garnering many thousands of citations each – indicating that they can be highly influential in setting the direction of policy and research. Unfortunately, many 'global' reviews suffer from severe geographic and taxonomic biases that may preclude a comprehensive understanding of how climate change is impacting Earth's natural systems (Lenoir & Svenning, 2015).

GEOGRAPHIC BIASES IN GLOBAL REVIEWS

Approximately 1/3 of the Earth's land surface lies within the tropics (23.4° S – 23.4° N), and given the latitudinal species gradient, the vast majority of Earth's species are tropical. Tropical ecosystems are, however, essentially absent from nearly all major climate change studies and reviews conducted to date. For example, in their landmark review claiming to have identified 'globally coherent fingerprints of climate change', Parmesan & Yohe (2003) reviewed the effects of climate change on the phenologies of nearly 200 species – none of which were from latitudes below 42.5° (the approximate latitude of Boston, MA, USA, or Rome, Italy). Collectively, Walther *et al.* (2002) and Parmesan (2006) synthesized more than 800 terrestrial and marine studies from around the world but included only a single study from the tropics. Similarly, Root *et al.* (2003) reviewed more than 150 studies of nearly 1500 species but included none from the tropics. Poloczanska *et al.*'s (2013) review of the 'global imprint of climate change on marine life' included only scant information from the tropics (35

of 1323 species responses = 2%) as did Brown *et al.*'s (2016) review of studies assessing distributional and phenological responses of marine species (the review of distributional responses included 418 species of which 61 [14.6%] were tropical, and the review of phenological responses included 109 species – none of which occur at latitudes below 32° which is the approximate latitude of Dallas, TX, USA, or Shanghai, China). Likewise, Pearce-Higgins *et al.* (2015) reviewed studies assessing the responses of more than 230 terrestrial species to long-term changes in temperature and precipitation. While the explicit goal of their study was to 'examine global patterns in the response of species' populations to climate variables', only 19 species (8% of study species) from latitudes below 30° and only 4 species (<2% of study species) from tropical latitudes were included. While the lack of available studies from the tropics is perfunctorily acknowledged in some (but not all) of these studies, the impacts of this bias are rarely discussed (but see Lenoir & Svenning, 2015).

The absence of tropical species from most global syntheses is especially dangerous because tropical species are expected to have fundamentally different responses to climate change than their temperate counterparts. For example, one of the major predictions for how species will respond to climate change is through 'species migrations' in which species shift their ranges to remain at equilibrium with suitable climatic conditions (Thuiller, 2007). Supporting these predictions, Chen *et al.* (2011) conducted a large meta-analysis which indicated that most studied species are in fact shifting their distributions and that these shifts are generally on pace with rates of regional warming. This meta-analysis included over 2100 species' responses as documented in more than 23 separate studies. Only 160 species responses from 2 studies (8% of species' responses and studies) were from the tropics. More recently, Lenoir & Svenning (2015) conducted a comprehensive review of climate change-driven range shifts as documented in over 200 studies – only 7% (16 studies) of which represented tropical species. Can we really hope to draw general conclusions about species' responses to climate change given such a poor representation from the tropics?

In fact, there is good reason to predict that most tropical species will be less capable than temperate species of keeping pace with climate change through species migrations (Feeley *et al.*, 2015; Perez *et al.*, 2016). The absence of a latitudinal temperature gradient within the tropics (Wright *et al.*, 2009) eliminates pole-ward migrations – a well-supported option for temperate species – as a possibility for most equatorial species. Also, many temperate communities are the product of rapid migrations and range expansions following past glacial retreats (Willig *et al.*, 2003). Consequently, at least some temperate species are likely to have behavioural and/or physiological adaptations that can facilitate rapid dispersal and range shifts. Such pre-adaptations for range shifts are predicted to be less common in species from the tropics where the climates and ecosystems have remained relatively stable through time. Finally, a higher number and proportion of species in the tropics rely on interspecific interactions for

dispersal and reproduction (Bawa, 1990), increasing the difficulty of species migrations. Regrettably, these predictions remain tentative given the few studies of migrations in the tropics and especially in the lowland tropics (Feeley *et al.*, 2012; Lenoir & Svenning, 2015) Rehm, 2014.

TERRESTRIAL VERSUS MARINE BIASES IN GLOBAL REVIEWS

Another pervasive geographic bias is the tendency for global reviews of climate change impacts to focus disproportionately on terrestrial ecosystems and species. Most of the reviews mentioned above include both terrestrial and marine species, but there is a clear predominance of land species. As examples, the review of Chen *et al.* (2011) was focused heavily on terrestrial species but included 2 studies representing a total of 47 marine species (37 algae from Portugal, 10 intertidal molluscs from Chile), and of the hundreds of species included in Parmesan & Yohe's (2003) and Root *et al.*'s (2003) reviews of phenological responses to climate change – all but one (a marine zooplankton from the north Pacific) were terrestrial species. The authors of these studies provided no mention of these disparities nor any discussion of how it may have influenced their results and interpretations. The bias towards terrestrial versus marine systems in most global reviews is both noteworthy and surprising given that the majority of the biosphere is marine, many marine species are highly vulnerable to climate change (e.g. through coral bleaching; Hoegh-Guldberg *et al.*, 2007), and that there are actually a fair number of studies assessing the responses of marine species to climate change (e.g. Poloczanska *et al.* (2013); Lenoir & Svenning (2015) and Brown *et al.* (2016), reviewed more than 208, 89 and 79 studies, respectively, documenting the responses of marine species to climate change).

TAXONOMIC BIASES IN GLOBAL REVIEWS

Beyond geographic biases, most climate change studies also suffer from severe taxonomic biases. The majority of studies included in global reviews are of animals. Within animals, there is a very strong bias towards vertebrates (despite the fact that most animals are invertebrates) and especially towards charismatic endotherms such as mammals and birds (Lenoir & Svenning, 2015). As just one example, of the 19 animal and plant species from latitudes $\leq 30^\circ$ included in Pearce-Higgins *et al.* (2015), 15 are mammals (12 large African ungulates, 2 rodents and 1 lemur). Ectothermic vertebrate species, generally considered to be more thermally fragile and at elevated risk of range contractions or extinctions from climate change (Tewksbury *et al.*, 2008; Gunderson & Stillman, 2015), are largely absent from global meta-analyses. Amphibians are scantily represented in the major reviews. Reptiles, and especially lizards – considered to be particularly vulnerable to climate change (Sinervo *et al.*, 2010) – are often absent altogether.

Plants are not only grossly underrepresented in most of the global reviews of climate change impacts (e.g. only 20 of

the 87 species included in Root *et al.*'s (2003) review of phenological responses to climate change were plants and Chen *et al.* (2011) included no plants in their review of latitudinal range shifts), but when they are included, plants are almost always collated into a single kingdom-level group. In other words, although detailed subcategorization is the standard for Animalia (typically to at least the class level), the same treatment is not afforded to plants, regardless of large disparities in the phylogenetic histories and/or ecologies of the included species. Different plant taxonomic and functional groups are expected to respond differently to climate change, and indeed many coupled climate Earth system models break vegetation into at least a small number of plant functional types (forest, grasslands, etc.) (Sakschewski *et al.*, 2015). There is a clear need for the studies synthesizing the impacts of climate change on Earth's systems to align with the same level of taxonomic and/or functional resolution as used in our leading climate models. As one example of how plant functional groups may be expected to respond differently, general photosynthetic theory predicts that C3 species will gain a competitive edge over C4 grass species in higher concentrations of atmospheric CO₂ (Ehleringer *et al.*, 1991). However, increasing global temperatures may promote expansion of C4 species, which have higher thermal optima for photosynthesis than C3 plants (Angelo & Daehler, 2013; Yamori *et al.*, 2013). It is troubling to realize that while differential responses such as these are built into many models, we cannot refute or support model predictions due to a lack of sufficient evidence of how individual plant species, or even distinct functional groups, are actually responding to climate change.

CALLING FOR AN HONEST ASSESSMENT OF THE DATA'S SCOPE

It is absolutely critical that we understand the effects of climate change on natural systems if we ever hope to accurately forecast, or eventually mitigate, changes in diversity and ecosystem function. Large-scale reviews and meta-analyses, such as the examples described above, are very useful and powerful tools for synthesizing available information – making it palatable for the general public and policymakers. Unfortunately, the information currently available for most ecosystems and species remains woefully sparse, leading to geographic and taxonomic biases in any subsequent reviews. Despite being pervasive and profound, these biases often go unrecognized (but see Lenoir & Svenning, 2015; Brown *et al.*, 2016) and reviews are too often explicitly or implicitly presented as being 'global' in scale. Indeed, in many cases the taxonomic and geographic information of the included species is not openly provided or is only available within online supplemental materials. Failure to forthrightly present, adequately acknowledge and effectively account for biases in the data is potentially misleading; we can be fooled into thinking that we have found global signatures of climate change when in fact any synthetic conclusions that we do have are mostly based on just a small subset of species –

species that are unlikely to be representative of global patterns. Importantly, if we fail to recognize taxonomic and geographic biases, then there will be little motivation to initiate or fund new studies to gain information on understudied species and systems. In order to fix this problem and advance our understanding of how climate change is impacting natural ecosystems, we need to first take an honest assessment of the scope of data that are and are not available; only then can we start to correct these biases through directed studies and initiatives.

ACKNOWLEDGEMENTS

We thank Jonathan Lenoir and an anonymous referee for valuable comments on a previous version of this manuscript. The authors' research is funded through the US National Science Foundation (DEB-1350125). At the time of writing, KJF was supported under a Fulbright Colombia Research Fellowship and TMP was supported under a graduate fellowship of FIU's International Center for Tropical Botany.

REFERENCES

- Angelo, C.L. & Daehler, C.C. (2013) Upward expansion of fire-adapted grasses along a warming tropical elevation gradient. *Ecography*, **36**, 551–559.
- Bawa, K.S. (1990) Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics*, **21**, 399–422.
- Brown, C.J., O'Connor, M.I., Poloczanska, E.S., Schoeman, D.S., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Pandolfi, J.M., Parmesan, C. & Richardson, A.J. (2016) Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Global Change Biology*, **22**, 1548–1560.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Ehleringer, J.R., Sage, R.F., Flanagan, L.B. & Pearcy, R.W. (1991) Climate change and the evolution of C4 photosynthesis. *Trends in Ecology and Evolution*, **6**, 95–99.
- Feeley, K.J., Rehm, E.R. & Machovina, B. (2012) The responses of tropical forest species to global climate change: acclimate, adapt, migrate, or go extinct? *Frontiers of Biogeography*, **4**, 69–82.
- Feeley, K.J., Silman, M.R. & Duque, A. (2015) Where are the tropical plants? A call for better inclusion of tropical plants in studies investigating and predicting the effects of climate change. *Frontiers of Biogeography*, **7**, 174–176.
- Gunderson, A.R. & Stillman, J.H. (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20150401.
- Hoegh-Guldberg, O., Mumby, P.J., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga,

- N., Bradbury, R.H., Dubi, A. & Hatzios, M.E. (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.
- Lenoir, J. & Svenning, J.-C. (2015) Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, **38**, 15–28.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pearce-Higgins, J.W., Ockendon, N., Baker, D.J., Carr, J., White, E.C., Almond, R.E.A., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Butchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E., Sutherland, W.J. & Tanner, E.V.J. (2015) Geographical variation in species' population responses to changes in temperature and precipitation. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20151561.
- Perez, T.M., Stroud, J.T. & Feeley, K.J. (2016) Thermal trouble in the tropics. *Science*, **351**, 1392–1393.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V. O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A. & Richardson, A.J. (2013) Global imprint of climate change on marine life. *Nature Clim. Change*, **3**, 919–925.
- Rehm, E.M. (2014) Rates of upslope shifts for tropical species depend on life history and dispersal mode. *Proceedings of the National Academy of Sciences USA*, **111**, E1676.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57.
- Sakschewski, B., Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peñuelas, J. & Thonicke, K. (2015) Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology*, **21**, 2711–2725.
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B. *et al.* (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science*, **328**, 894–899.
- Tewksbury, J.J., Huey, R.B. & Deutsch, C.A. (2008) Ecology: putting the heat on tropical animals. *Science*, **320**, 1296–1297.
- Thuiller, W. (2007) Biodiversity: climate change and the ecologist. *Nature*, **448**, 550–552.
- Walther, G.R., Post, E., Convey, P., Menzel, A. & Parmesan, C. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 273–309.
- Wright, S.J., Muller-Landau, H.C. & Schipper, J. (2009) The future of tropical species on a warmer planet. *Conservation Biology*, **23**, 1418–1426.
- Yamori, W., Hikosaka, K. & Way, D.A. (2013) Temperature response of photosynthesis in C3, C4, and CAM plants: temperature acclimation and temperature adaptation. *Photosynthesis Research*, **119**, 101–117.

BIOSKETCHES

Kenneth Feeley is the Smathers Chair of Tropical Tree Biology in the University of Miami's Department of Biology (at the time of writing he was based at Florida International University). His research focuses on understanding how the structure, dynamics, composition and geographic distribution of tropical forests (and their constituent species) are affected by large-scale anthropogenic disturbances such as climate change, deforestation and habitat fragmentation.

Timothy Perez and **James Stroud** are doctoral students at the University of Miami and Florida International University, respectively (at the time of writing both students were based at Florida International University). Tim Perez' research is focused on understanding the thermal ecology and physiology of tropical plant species. James Stroud studies the patterns and process of community assembly, and the factors allowing for species coexistence in diverse lizard assemblages.

Author contributions: All authors conceived the idea for this study, compiled and analysed the data and wrote the manuscript.

Editor: Ingolf Kühn