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Vulnerability to climate change increases with trophic level in terrestrial organisms

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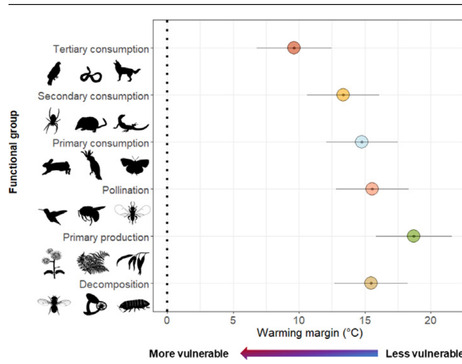
HIGHLIGHTS

- First study to compare the physiological vulnerability of terrestrial functional groups to climate change.
- Comprehensive analysis of 1,701 species upper thermal limits across the globe.
- Evolutionary history and upper thermal limit methodology considered within vulnerability models.
- Tertiary consumers were the most vulnerable group to climate change and primary producers were the least vulnerable.
- Impacts of climate change are likely to be non-random with respect to the function roles that species play in ecosystems.

GRAPHICAL ABSTRACT



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ABSTRACT

The resilience of ecosystem function under global climate change is governed by individual species vulnerabilities and the functional groups they contribute to (e.g. decomposition, primary production, pollination, primary, secondary and tertiary consumption). Yet it remains unclear whether species that contribute to different functional groups, which underpin ecosystem function, differ in their vulnerability to climate change. We used existing upper thermal limit data across a range of terrestrial species (N = 1701) to calculate species warming margins (degrees distance between a species upper thermal limit and the maximum environmental temperature they inhabit), as a metric of climate change vulnerability. We examined whether species that comprise different functional groups exhibit differential vulnerability to climate change, and if vulnerability trends change across geographic space while considering evolutionary history. Primary producers had the broadest warming margins across the globe (μ = 18.72 °C) and tertiary consumers had the narrowest warming margins (μ = 9.64 °C), where vulnerability tended to increase with trophic level. Warming margins had a nonlinear relationship (second-degree polynomial) with absolute latitude, where warming margins were narrowest at about 33°, and were broader at lower and higher absolute latitudes. Evolutionary history explained significant variation in species warming margins, as did the methodology used to estimate species upper thermal limits. We investigated if variation in body mass across the trophic levels could explain why higher trophic level organisms had narrower warming margins than lower trophic level organisms, however, we did not find support for this hypothesis. This study provides a critical first step in linking individual species vulnerabilities with whole ecosystem responses to climate change.

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1. Introduction

The functional roles species play in ecosystems such as decomposition, primary production, consumption, and pollination scale up to support ecosystem function (Box 1) (Crowther et al., 2015; Enquist et al., 2003, 2015). As climates change and species respond individually via shifts in geographical range, phenology or population abundance, we will observe alterations in functional group (Box 1) interactions and species compositions, which are anticipated to have major effects on ecosystem function (Harvey et al., 2020; Oliver et al., 2015; Voigt et al., 2003). The robustness of ecosystem function to climate change will depend, in part, on the diversity of species that contribute to each functional role (functional redundancy) (García et al., 2018; Hisano et al., 2018; Loreau, 2000). With greater species diversity there is an increased likelihood that some species will be resilient to warming climates, decreasing the likelihood that functional roles within ecosystems will be lost to climate change. However, if the vulnerability of species that contribute towards different functional groups within ecosystems is non-equal, we might observe declines in ecosystem function at a more accelerated rate than we would expect based on individual species vulnerabilities to climate change (i.e. response diversity) (Dell et al., 2014; Elmqvist et al., 2003; Mori et al., 2013; Thackeray et al., 2016; Thakur, 2020; Voigt et al., 2003).

Ecological hypotheses predict that species that contribute towards higher trophic levels should be more vulnerable to climate change than lower trophic level species (Thackeray et al., 2016; Voigt et al., 2003). This is because large and highly active species (with high metabolic rates) are expected to lose the ability to maintain their energetic requirements under hot conditions faster than smaller and less active species (Brown et al., 2004; Huey and Kingsolver, 2019; Peralta-Maraver and Rezende, 2021; Vasseur and McCann, 2005; Voigt et al., 2003). In addition, species that contribute towards lower trophic levels have a greater ability to shift their phenologies with climate change than higher trophic level species, potentially buffering them from warming temperatures (Thackeray et al., 2016). However, it remains unclear whether species that contribute towards different functional groups have different physiological vulnerabilities (e.g. upper thermal limits) to climate change, especially in the terrestrial realm (but see a marine example by Hu et al. (2022)). Understanding how species upper thermal limits vary across the functional groups they contribute to can provide key information on functional group rank vulnerability, and accordingly, which functional groups are likely to limit ecosystem function first with further climate warming.

Species upper thermal limits can be estimated via tolerance assays (ramping or static) or thermal performance curves (including estimations up upper limits of the thermal neutral zone in endotherms) (Angilletta, 2009; Bennett et al., 2021; Diamond et al., 2012; Kellermann et al., 2012; Sunday et al., 2014). Upper thermal limits can then be compared to current or future environmental temperature yielding a 'warming margin', or the temperature difference between a species upper thermal limit and the maximum environmental temperature they experience. Owing to their composite nature, warming margins can vary according to properties of the environment and properties of the organism (Kellermann et al., 2012; Sunday et al., 2014). In aggregate, warming margins identify the species or populations that inhabit environments close to their physiological capacities and thus are most vulnerable to climatic change (Kellermann et al., 2012; Sunday et al., 2014).

Box 1
Glossary.

Ecosystem function: fluxes of energy, nutrients and organic matter through an environment which in turn supports ecosystem productivity and stability (Crowther et al., 2015; Enquist et al., 2003, 2015).
Functional groups: a group of species that contribute towards a certain *functional role* within an ecosystem such as: primary production, consumption (primary, secondary or tertiary), pollination and decomposition. We use the term functional group in the same way that Voigt et al. (2003) uses trophic level, however, because we also included pollinators in our analysis (which we consider to be fundamental for ecosystem function, but is not a trophic level) we use the term *functional group* instead.
Warming margin: the distance between an organism's upper thermal limit and their (average warmest month) maximum environmental temperature. Species vulnerabilities to climate change increase with decreasing warming tolerance.

We appreciate that thermal limits and warming margins are estimated with caveats (e.g. variation in experimental methodologies), as highlighted in a number of manuscripts (Allen et al., 2016; Clusella-Trullas et al., 2021; Diamond and Yilmaz, 2018; Hoffmann et al., 2013). Here, we assume that thermal limits and their associated warming margins are a reasonable proxy for species vulnerabilities to climate change. This assumption is supported by findings that species' upper thermal limits are correlated with warming-induced range shifts and extinctions (Comte et al., 2014; Diamond et al., 2012; Pinsky et al., 2019; Sinervo et al., 2010). We have also assumed that estimates of warming margins are static and unable to shift via evolution or plasticity. We appreciate that this is unlikely to be the case, but sufficient data do not currently exist to factor evolutionary potential or plasticity of thermal tolerance into our models. Nevertheless, the extent to which either plasticity or selection on heritable genetic variation will shift upper thermal limits is expected to be small (Gunderson and Stillman, 2015; Kellermann and van Heerwaarden, 2019).

Comparisons of species warming margins across spatial scales allows assessments of which geographic regions, such as temperate vs tropical, are most likely to lose species or populations to climate change. Whether tropical or temperate species are more vulnerable to climate change has generated great debate over the past 20 years, as species that inhabit tropical environments sit closer to their upper thermal limits on average, but temperate environments often experience higher extreme summer temperatures which have the potential to adversely impact populations (Deutsch et al., 2008; Helmuth et al., 2002; Kellermann et al., 2012; Kingsolver et al., 2013; Sunday et al., 2014). While warming margins have been compared across species and latitude in the past, it is not known if species that contribute towards certain functional roles are more vulnerable than others, and if trends in functional group vulnerability changes with variation in species composition across ecosystems. Loss of certain functional roles in ecosystems could impose trophic cascades under climate change, potentially reducing ecosystem function (Thakur, 2020; Voigt et al., 2003).

We tested if species that contribute to different functional groups have different vulnerabilities to climate change by leveraging large, compiled datasets of terrestrial species thermal tolerance and categorised each species into their principal functional group across the globe (tertiary, secondary, and primary consumption, pollination, primary production, decomposition) (we refer to this analysis as the 'global' analysis for simplicity, however we acknowledge the deficit of high latitude data points (>66° of latitude), which means this is not a truly 'global' analysis) (Fig. 1). To compare the vulnerability of species that contribute to different functional groups, we calculated each species' warming margin, and assessed how warming margins varied across functional groups and absolute latitude. To provide nuance to the debate on whether tropical or temperate species are the most vulnerable to climate change, we examined how functional group vulnerability changes across low- and mid-latitude regions. Furthermore, to explore if trends in functional group vulnerability are maintained across geographic scale, and with changes in species composition across ecosystems, we compared global vulnerability trends with regional trends (low- vs mid-latitude).

We examined two main research questions on terrestrial organisms. 1) Do species that contribute towards different functional groups vary in their vulnerability to climate change at a 'global' level? 2) Does functional group vulnerability differ across tropical and temperate regions, and how

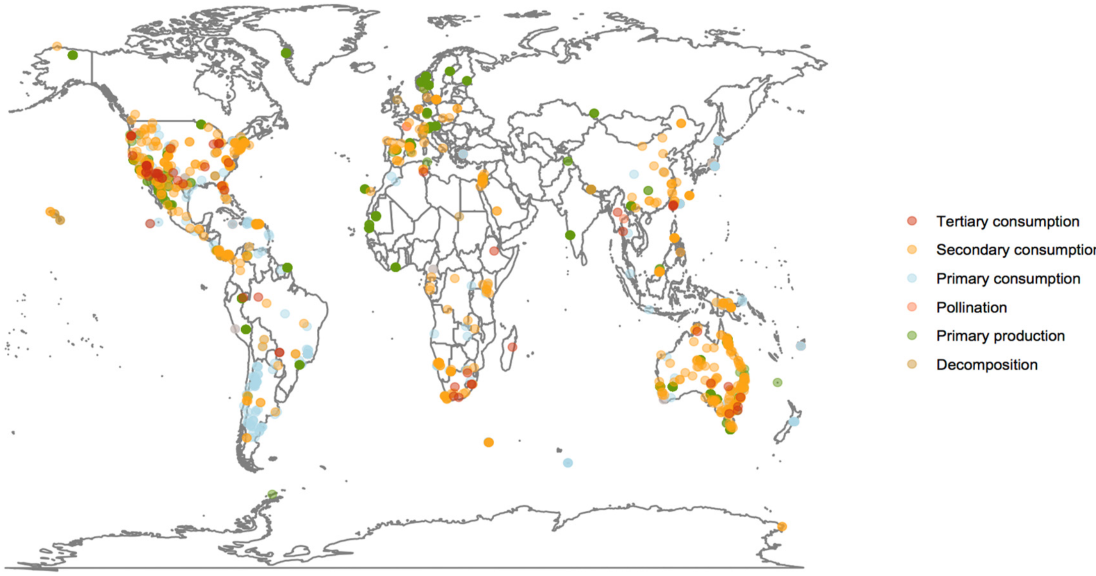

Fig. 1. Collection locations of terrestrial species upper thermal limit data across the globe (N = 2140). Points are coloured by the functional group that species contribute to. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

do regional vulnerability trends compare to global vulnerability trends? Finally, we discuss the limitations of our dataset and analyses, and discuss research priorities for the future.

2. Materials and methods

We compared upper thermal limit data of terrestrial species from two large databases; the updated GlobTherm (Bennett et al., 2018) dataset published by Sunday et al. (2019), and the Lancaster and Humphreys (2020) dataset. Pollinators, decomposers and tertiary consumers were underrepresented within these databases, so we filled in thermal tolerance data gaps by searching a set of specific search criteria for each functional group on Web of Science (https://www.webofscience.com/wos/woscc/basic-search) (see Supplementary Material Section 1 for search criteria, search results and PRISMA flow diagram). Our searches found 184 published manuscripts, however, only 18 were suitable for inclusion in the analysis (studies needed to provide collection GPS coordinates, be on terrestrial species, collect organisms from the wild, test upper thermal limits, and the study must have been on either a pollinator, decomposer or tertiary consumer). From these studies we collected data on organismal thermal tolerance, what kind of experimental methodology was used, the GPS coordinates species were collected from, and whether the organism was a plant, fungi, ectotherm or endotherm. Thermal tolerance data was only compared across animals in their adult/later life stages. Some organisms with aquatic larval stages were included (e.g. some amphibians), however, they were only included in the analysis if the thermal tolerance data was on their adult life stage. A full systematic review of all terrestrial species' upper thermal limits was not conducted as this was accomplished already by the updated version of GlobTherm (Sunday et al., 2019) and Lancaster and Humphreys (2020). In total, we compared 2140 upper thermal limit data points across 6 functional groups (decomposers, primary producers, pollinators, primary consumers, secondary consumers, and tertiary consumers), and 1701 species (Fig. 1; Table 1). Some species had upper thermal limit data for more than one location and thus occurred in the dataset more than once. Missing taxonomic information for species was extracted from the National Centre for Biotechnology Information database (https://www.ncbi.nlm.nih.gov/taxonomy) using the Taxize package (Chamberlain and Szöcs, 2013) in the statistical program R version 4.1.0 (R Core Team, 2022). These large databases include upper thermal limit estimates obtained using a variety of methodologies such as dynamic, static, and upper edge of the thermal neutral zone (TNZ) which we acknowledge could influence upper thermal limit estimations (Allen et al., 2016; Diamond and Yilmaz, 2018). Dynamic methodologies estimate the temperature at which an organism starts to spasm or lose equilibrium (Tcrit), loss of movement (Tmax/ct), or the temperature at which the organism dies (lethal temperature (lt)) (however these terms are used in a variety of ways in the literature), using a range of ramping rates in each category (0.0167–3.6 °C per minute). Static methodologies estimate the temperature at which 50 % (LT50/T50) or 100 % (LT100) of the individuals within a study die, lose physiological function, or stop growing (max growth temperature). The upper edge of the thermal neutral zone measures the maximum temperature at which an endothermic animal can no longer maintain homeostatic body temperature without producing excess metabolic heat (Sunday et al., 2019). Accordingly, we included methodology (9 levels) as a random factor within our analysis (we include a summary of the methodology categories (static, dynamic and TNZ) used per functional group in Table 1).

We categorised species into functional group trophic level categories as per Reichle (2019). For simplicity, species were categorised into functional groups based on their predominant adult life stage energy sources to the family level, i.e. autotrophs were labelled primary producers and species in families that predominantly eat primary producers were considered primary consumers. Species in families that predominantly eat primary consumers were considered secondary consumers and those that eat secondary consumers were considered tertiary consumers. Species in families with known decomposition and pollination roles were also categorised accordingly. However, some species were considered both primary consumers and pollinators and thus appear twice in the dataset. We assessed how functional group vulnerability in the above categories differs across a 'global' scale (where absolute latitude was included as a predictor variable) and regional (low 0–23.1° vs mid 23.1–46° latitudes) scale.

2.1. Analysis

Analyses were performed in the statistical program R version 4.1.0 (R Core Team, 2022). Warming margins for each species were calculated by subtracting the maximum environmental temperature (BioClim variable 5 at a 30 s resolution between the years 1970–2000) (Fick and Hijmans, 2017) at each species collection location from each species upper thermal limit (upper thermal limit - maximum environmental temperature = warming margin). Maximum environmental temperatures for soil dwelling organisms such as fungi and termites (n = 40 soil dwelling decomposer species) were extracted from a soil depth of 10 cm using the NicheMapR

Table 1
Summary of the taxa and the methodology categories used to estimate upper thermal limits within each functional group within the global analysis.

Functional group	Class	Count
Tertiary consumption		57
Dynamic		31
	Lepidosauria	31
TNZ		26
	Aves	11
	Mammalia	15
Secondary consumption		594
Dynamic		423
	Amphibia	108
	Arachnida	20
	Archelosauria	2
	Insecta	139
	Lepidosauria	154
Static		3
	Arachnida	2
	Lepidosauria	1
TNZ		168
	Aves	58
	Mammalia	110
Primary consumption		349
Dynamic		191
	Insecta	99
	Lepidosauria	92
Static		32
	Insecta	32
TNZ		126
	Aves	36
	Mammalia	90
Pollination		118
Dynamic		81
	Insecta	81
Static		31
	Insecta	31
TNZ		6
	Aves	6
Primary production		945
Dynamic		384
	Ginkgoopsida	1
	Magnoliopsida	358
	Pinopsida	22
	Polytrichopsida	1
	Spermatophyta	2
Static		561
	Bryophyta	1
	Bryopsida	3
	Jungermanniopsida	12
	Magnoliopsida	497
	Pinopsida	15
	Polypodiopsida	27
	Sphagnopsida	6
Decomposition		77
Dynamic		23
	Insecta	18
	Lecanoromycetes	3
	Malacostraca	2
Static		54
	Euascomycetes	1
	Eurotiomycetes	18
	Insecta	34
	Malacostraca	1
Tertiary consumption		57

package (Kearny and Porter, 2019). The latitudinal extents of each functional group were checked prior to analyses to ensure functional group warming margins were comparable, i.e. each functional group had species collected from a broad span of latitudes (Supplementary Fig. 1). Due to the lack of thermal limit data collected above 66° latitude, and an uneven sample of functional groups at high latitudes, we limit our global analysis to between the equator and 66° (absolute) latitude (Fig. 1, Supplementary Fig. 1). Error/variance in upper thermal limit estimates were not reported broadly or consistently across datasets and thus we were unable to perform error propagation analysis throughout the models.

2.2. Global analysis

We examined trends in global species warming margins and how they differ across functional groups and absolute latitude using linear mixed effect models in the lme4 package (Bates et al., 2007). We used a model comparison approach, inspired by a strong inference framework, to test three hypotheses: 1) functional group and absolute latitude (as a continuous variable) together explain variation in species warming margins, 2) functional group explains most variation in species warming margins, 3) functional group does not explain variation in species warming margins, but absolute latitude does. We also examined whether model fit was better if absolute latitude was modelled as a second-degree polynomial as we observed that the relationship between warming margin and absolute latitude had a curved nature when plotted. To consider variation in the methodology used to estimate species upper thermal limits, methodology was included as a random factor within our models (9 levels). We also examined whether trends in functional group upper thermal limits mirrored patterns in warming margins across species using the same model structure as the best fitting warming margin model (Supplementary Table 3).

To take phylogenetic non-independence into account, we included nested species taxonomic classification (Class/Order) as a random factor into our models, similar to studies by Lenoir et al. (2020) and Sunday et al. (2011). Phylum was excluded in the nested taxonomic classification random effect because there was only one level of phyla within the organisms that contributed towards primary production and tertiary consumption, thus phylum is confounded with functional group. Similarly, as we grouped species to functional group from the family level, family and genus were also confounded and were not included in the nested taxonomic classification random effect structure. We compared the Akaike Information Criterion (AIC) of each model to determine which hypothesis offered the greatest relative support for understanding the variation in species warming margins as per Burnham and Anderson (2002). We also compared each of the three hypotheses with and without the inclusion of testing methodology and taxonomic classification as random factors, however, models that included the full random effect structure always performed the best (Supplementary Table 2).

While we were unable to conduct a phylogenetic analysis on all of the species in our dataset, we did conduct a phylogenetic analysis on a subset ($n = 940$) of the organisms in our dataset to ensure our findings were robust (Supplementary data set 2). A phylogenetic tree was constructed using TimeTree (Kumar et al., 2022) and we used the phyr package (Li et al., 2020) to conduct a phylogenetic generalised linear mixed model (with Brownian motion evolution) to examine whether our findings from the main global analysis model remained consistent (Supplementary Analysis 1). We used the same model structure as the best fitting linear mixed effect model (where warming margin was the response variable, functional group and absolute latitude (as a second-degree polynomial) were the predictor variables and experimental methodology and phylogeny were included as random factors). Phylogenetic signal was calculated using the phylosig function from the phytools package (Revell, 2012).

We did not include thermogenic capacity (ectothermic animal, endothermic animal, plant and fungi) as a predictor variable in our main analysis because we have already accounted for variation attributed to organism type with nested taxonomic classification as a random factor. However, we appreciate that thermogenic capacity does explain variation in species thermal limits and warming margins as previously described by Bennett et al. (2021) and Sunday et al. (2011 & 2014). Thus, we conducted an additional analysis to examine the effect thermogenic capacity had on warming margins by including functional group, absolute latitude and thermogenic capacity as predictor variables and testing methodology as a random factor, but excluded nested taxonomic classification as a random factor. We also appreciate that many groups of species are likely to be under-represented within the dataset, and that biases towards upper thermal limit experiments on certain species could impact our findings. We have, however, compared the broadest dataset of upper thermal limits that currently exists in terrestrial species in an attempt to analyse the most unbiased and diverse dataset of species warming margins possible.

Furthermore, we have included a table that explicitly lists all of the classes of organisms that contribute towards each functional group, the methodology that was used to estimate their upper thermal limits and their count data to outline where biases might occur (Table 1).

We explored whether trends in species warming margins across functional groups could be explained by variation in organismal body mass across the functional groups. We extracted body mass for as many species in our database as possible from four recently published large databases/meta-analyses which examine variation in species body mass (Leiva et al., 2019; Herberstein et al., 2022; Peralta-Maraver and Rezende, 2021; White et al., 2022). We extracted body mass data for 417/1701 species in our dataset (tertiary consumers (n = 20), secondary consumers (n = 164), primary consumers (n = 138), pollinators (n = 56), decomposers (n = 39)) (Supplementary data set 3). We used a linear mixed effect model to determine if species warming margins were explained by an interaction between body mass and functional group, and a fixed effect of absolute latitude as a second-degree polynomial. We $\log_{10}$ transformed body mass because body mass was on different scales for different organism types. We included thermal tolerance methodology as a random factor as well as nested taxonomic classification.

2.3. Regional analysis

While we included absolute latitude as a predictor variable within our 'global' analysis, we wanted to separately examine how functional group vulnerability might change across broad scale regions (tropical vs temperate) with different species compositions. Therefore, to compare functional group vulnerability on a regional scale we split species into low- or mid-latitude regions, where species with collection latitudes between absolute latitudes 0° and 23° were categorised as low-latitude, and species with absolute collection latitudes between 23.1° and 46° were categorised as mid-latitude (the mid-latitude region was limited to 46° due to lack of data over 46° and so that the latitudinal breadths of each geographic region were equal). Using a linear mixed effect model, we examined how functional group vulnerability differed across broad scale geographic regions (low- and mid-latitude) by including an interaction between functional group and region in the model, as well as method and nested taxonomic classification as random factors.

Significance of effects in linear mixed effect models were assessed using a type II Wald Chi-squared test (in models without interactions) and a type III Wald Chi-squared test in models with interaction terms using the car package (Fox et al., 2012). We present estimated marginal means and standard errors calculated using the emmeans package (Lenth et al., 2018). Figures were produced using ggplot2 (Wickham, 2011).

2.4. Sensitivity analysis

To determine whether differences between functional group vulnerabilities were underpinned by sample size we conducted sensitivity analyses. We randomly sampled and bootstrapped warming margins (adjusted for testing methodology and evolutionary history) from each functional group within the global and regional datasets 10,000 times with sample sizes matching those found in the functional group with the smallest sample size (or region with the lowest sample size for each functional group for the regional analysis) using the sample function in base R. We then calculated functional group warming margin means and 95 % confidence intervals from the bootstrapped values and assessed whether they fell within the full dataset 95 % confidence intervals (conducted for the global and regional analyses).

3. Results

3.1. Global analysis

We compared 2140 warming margin estimates from 1701 species across six functional groups, where species from multiple taxonomic classes contributed to each functional group (Table 1).

The model that best explained variation in species warming margins across the globe included fixed effects of functional group and absolute latitude (as a second-degree polynomial), and random effects of upper thermal limit testing methodology and nested taxonomic classification (model R^2 = 0.78) (Supplementary Table 2). Warming margins varied across functional groups (χ^2 = 40.82, df = 5, P < 0.001), where warming margins tended to become narrower with increasing trophic level (except decomposers) (Fig. 2; Supplementary Table 3). Tertiary consumers had the narrowest warming margins (estimated marginal means) (9.63 ± 2.84 °C) and primary producers had the broadest warming margins (18.72 ± 2.89 °C) (Fig. 2) (estimated marginal means for all functional groups can be found in Supplementary Table 3). This pattern was mirrored in species upper thermal limits (Fig. 2), where tertiary consumers had the lowest upper thermal limits and primary producers had the highest upper thermal limits (χ^2 = 18.54, df = 5, P < 0.002) (Supplementary Table 3).

Absolute latitude (as a second-degree polynomial) played an important role in explaining variation in species warming margins (χ^2 = 715.41, df = 2, P < 0.001), where warming margins tended to be narrowest at mid-latitudes (around 33°), slightly broader at low latitudes, and quite broad at higher latitudes (Fig. 3). Nested taxonomic classification explained a significant amount of variation in species warming margins (χ^2 = 716.48, df = 1, P < 0.001) and so did the methodology used to estimate species upper thermal limits (χ^2 = 213.03, df = 1, P < 0.001). The phylogenetic analysis that was conducted on a subset (n = 940) of the species in the main dataset also found that functional group explained variation in species warming margins (χ^2 = 187.03, df = 1, P < 0.001) and the pattern of decreasing warming margins with increasing trophic level was maintained (Fig. 4; Supplementary Analysis 1). There was strong phylogenetic signal in warming margins across species (λ = 0.93, P < 0.001) (Fig. 4). These consistencies between analyses indicate that our findings from the global analysis are robust to sample size and how evolutionary history is accounted for (Supplementary Analysis 1).

Thermogenic capacity also explained a significant proportion of variation in species warming margins (χ^2 = 27.46, df = 2, P < 0.001) (however plants had to be removed from the model because all plants were primary producers causing the model to become rank deficient). Fungi had the broadest raw warming margins (n = 22, u = 34.56 °C) and endotherms had the narrowest warming margins (n = 326, u = 4.00 °C). Ectotherms (n = 847) had a mean warming margin of 12.99 °C and plants (n = 945) had a mean warming margin of 23.79 °C. Functional group (χ^2 = 207.93, df = 4, P < 0.001) and absolute latitude as a second-degree polynomial (χ^2 = 100.60, df = 1, P < 0.001) continued to explain large proportions of the variance in species warming margins in this additional analysis.

There was no overall effect of $\log_{10}$ body mass on species warming margins (χ^2 = 0.99, df = 1, P = 0.318) even though species in higher trophic levels had higher mean body masses than those in lower trophic levels (Table 2). There was also no interaction between $\log_{10}$ body mass and functional group (χ^2 = 3.91, df = 4, P = 0.418), where the trend of decreasing warming margins with increasing trophic level remained consistent irrespective of variation in body mass with functional groups. As with previous models, the effect of functional group (χ^2 = 13.23, df = 4, P = 0.001) and absolute latitude as a second-degree polynomial (χ^2 = 89.17, df = 1, P < 0.001) remained important in explaining variation in species warming margins. We also examined whether the trend of increasing vulnerability with trophic level could be explained by the high proportion of TNZ collected upper thermal limit data within the tertiary consumers (Supplementary Analysis 2) or the presence of nocturnal tertiary consumers (Supplementary Analysis 3). However, neither of these additional analyses pointed to a mechanism that could explain why warming margins become narrower with increasing trophic level. Finally, we found that global patterns in warming margins across functional groups were robust to sampling bias (95 % confidence intervals overlapped for each functional group when comparing modelled means and bootstrap means - Supplementary Table 4).

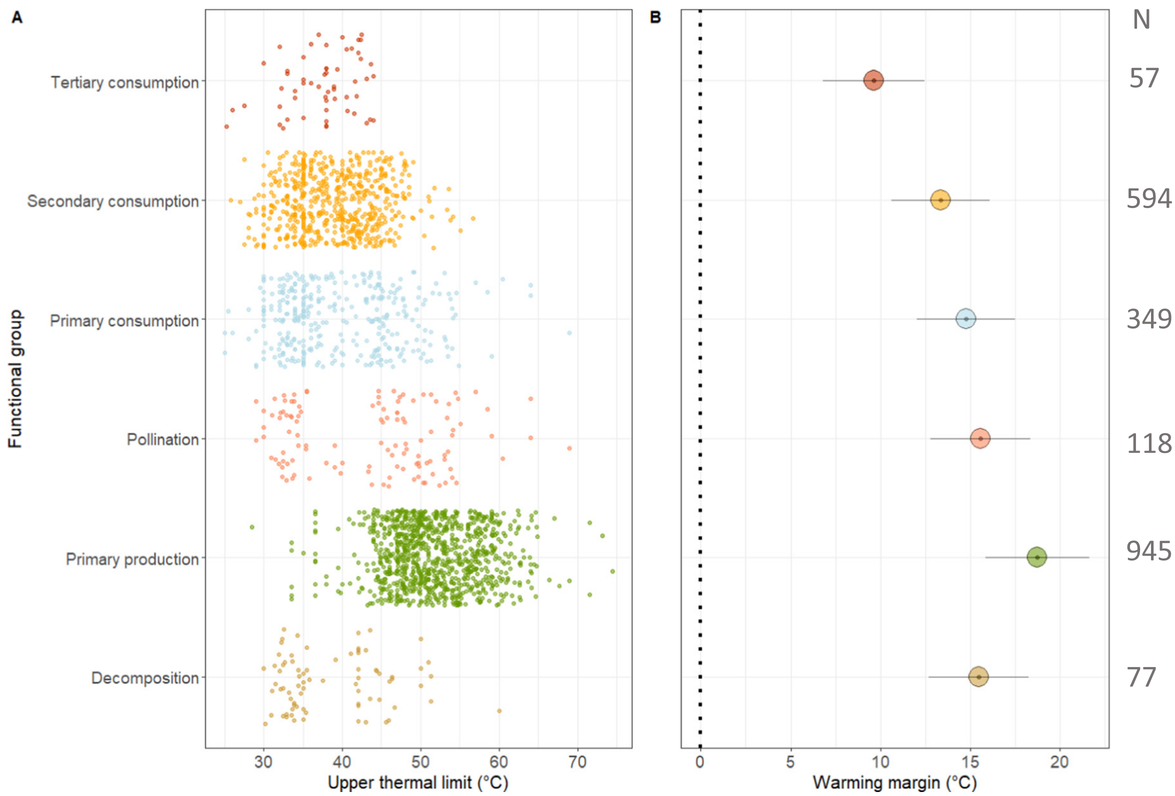

Fig. 2. (A) Global comparison of functional group upper thermal limits (raw) and (B) warming margin means and standard error (estimated model means which take evolutionary history and testing methodology into account) (degrees Celsius distance between upper thermal limit and maximum environmental temperature). Sample sizes (N) are located on the right-hand side of the figure. The dotted line represents a warming margin of 0.

3.2. Regional analysis

Functional group vulnerability differed between low- and mid-latitude regions (there was a significant interaction between functional group and region) (χ = 39.93, df = 5, P < 0.001). However, this trend was only driven by differences in warming margins within primary producers and primary consumers, where they had narrower warming margins in low-latitude regions than mid-latitude regions (pairwise contrasts between all other functional groups across regions were not significant) (Fig. 5; Supplementary Table 3). Similarly, to the global analysis, there was a general, but weaker, trend in increasing vulnerability (narrower warming margins) with increasing trophic level in both regions, however, there was little variation in warming margins within the consumer species in the low latitude region, potentially due to lower sample sizes (Fig. 2, Supplementary Table 3). Regional functional group vulnerability estimates were also robust to sampling bias, except for decomposers in low-latitude regions, likely due to low sample size of decomposers at low-latitudes (Supplementary Table 4).

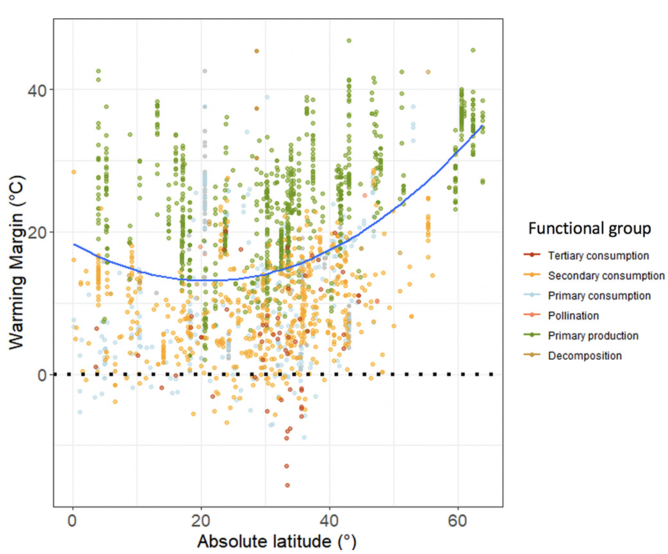

Fig. 3. Raw species warming margins across absolute latitude. Species are coloured by the functional group that they contribute to. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Understanding how climate change will influence biological systems, from individuals and species to whole ecosystems, is a key goal in ecology (Thakur, 2020; Traill et al., 2010; Tuff et al., 2016; Urban et al., 2016; Zarnetske et al., 2012). A first step towards this objective requires linking species and their physiological vulnerabilities to the functional groups that they contribute to within ecosystems.

At the global scale, warming margins tended to decrease with trophic level from primary producers (18.72 °C) to tertiary consumers (9.64 °C). This trend was observed when evolutionary history was accounted for by either including nested taxonomic information as a random factor or by conducting a phylogenetic generalised linear mixed model. Because evolutionary history is important in explaining variation in species warming margins, species diversity might only buffer loss of functional roles in ecosystems when species across highly divergent taxonomic groups contribute towards the same functional role within an ecosystem. In other words, the functional redundancy that arises from the species diversity in an ecosystem might be maximised by the co-occurrence of very distantly related taxa that contribute towards the same functional roles.

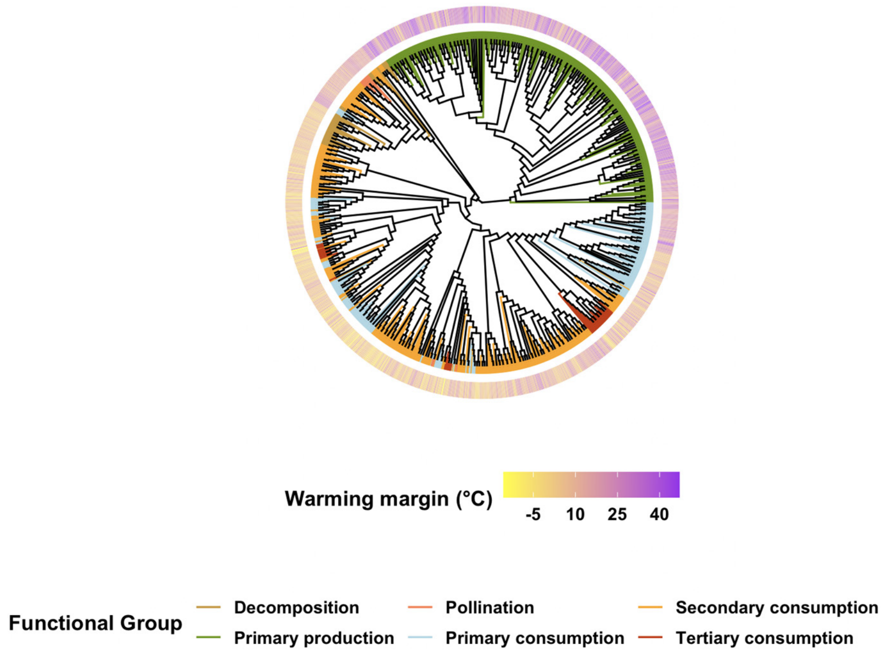

Fig. 4. Phylogenetic tree of species that contribute towards different functional groups (branch colour indicates functional group) and their associated warming margins indicated by bars on the outside of the tree (yellow indicates narrow warming margins and purple indicates broad warming margins). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Variation in body mass across functional groups in a subset of the organisms in the global dataset (n = 417).

Functional group	Mean body mass (g)	Standard error	N
Tertiary consumption	113.12	68.56	20
Secondary consumption	11.37	4.59	164
Primary consumption	0.62	0.19	138
Pollination	0.04	0.01	56
Decomposer	0.01	0.004	39

Variation among functional group warming margins appeared to largely reflect variation in upper thermal limits (Fig. 2). As species that contributed towards tertiary consumption had the lowest upper thermal limits and the narrowest warming margins, tertiary consumption might be the first functional role to limit ecosystem function across the globe. This finding supports ecological modelling and longitudinal species abundance monitoring studies that suggest vulnerability to climate change will differ across trophic levels, where top predators are likely to be the most at risk (Voigt et al., 2003; Zarnetske et al., 2012; Zhang et al., 2017). Loss of terrestrial top predators is likely to have prolific knock-on effects throughout ecosystems, where energy and mass cycles become unbalanced (Beschta and Ripple, 2009; Urban et al., 2016; Voigt et al., 2003; Zarnetske et al., 2012; Zhang et al., 2017). For example, the classic reintroduction of tertiary consumers (wolves) into Yellowstone National Park resulted in an increase in woody plants (from controlling the elk population) and an increase in other lower trophic level organism populations (Beschta and Ripple, 2009; Ripple and Beschta, 2012).

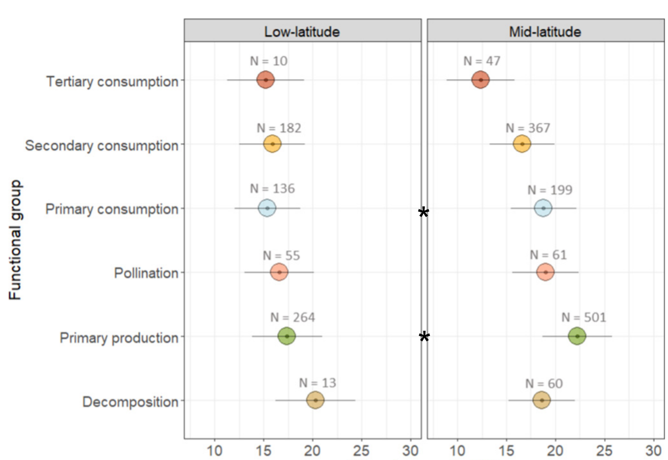

Fig. 5. Comparison of low- and mid-latitude functional group warming margin means and standard error (data adjusted to account for assay methodology and evolutionary history). Sample sizes (n) are indicated above each functional group warming margin mean. Asterisks between low- and mid-latitude functional groups indicate significant differences in warming margins between the regions.

While the terrestrial tertiary consumers in our analysis had the narrowest warming margins overall, at least some species contributing to each consumption group (tertiary, secondary and primary) had warming margins below 0 (Supplementary Fig. 2). This indicates that terrestrial consumer species are already inhabiting environments that experience temperatures higher than their upper thermal limits. It is possible that these species are already using behavioral thermoregulation for survival in their environment (Sunday et al., 2014). Indeed, behavioral thermoregulatory strategies are likely to vary across species, which could also impact trends in functional group vulnerability to climate change. For example, species that use physiological cooling mechanisms (e.g. evaporative cooling) might be less vulnerable to warming climates than species that need to move to cooler microhabitats to avoid suboptimal temperatures (but this is a relatively unexplored topic).

We examined whether variation in body mass across the functional groups could explain the pattern of narrowing warming margins with increasing trophic levels because ecological hypotheses predict that larger, more active species will be more vulnerable to warming climates due to an inability to maintain energetic requirements in hot conditions (metabolic meltdown) (Brown et al., 2004; Enquist et al., 2003; Hu et al., 2022; Huey and Kingsolver, 2019; Vasseur and McCann, 2005; Voigt et al., 2003; Peralta-Maraver and Rezende, 2021). However, an interaction between functional group and body mass did not explain variation in species warming margins (primary production was not included in this model). This finding was surprising because a recent study found that larger terrestrial organisms are less heat tolerant than smaller organisms and that thermal death occurs at relatively lower metabolic rates as body mass increases (Peralta-Maraver and Rezende, 2021). We also examined whether using the of upper limit of the thermal neutral zone as the estimate of thermal tolerance, or the presence of nocturnal species within the tertiary consumer dataset could explain the pattern of narrowing warming margins with increasing trophic level, however, we did not find support for either of these potential mechanisms (Supplementary Analysis 2 & 3).

Primary producers had very high upper thermal limits and broad warming margins on average compared to all other functional groups (Fig. 2). Primary producers might have evolved high upper thermal limits as a mechanism to survive in fluctuating environments as plants are stationary, and thus require the capacity to acclimate with thermal change or maintain broad thermal tolerances to survive with changes in environmental temperature (Huey et al., 2003). High thermal tolerances have also been observed in stationary developmental life stages of species such as *Drosophila* (Moghadam et al., 2019), supporting this idea. It is possible that such variation in life history traits could also explain why we observe slightly broader warming margins in pollinators than primary consumers in the global analysis, even though all pollinators are primary producers. For example, many pollinators like bees most commonly forage on warm and sunny days (Clarke and Robert, 2018), and because of this, perhaps they have evolved higher thermal tolerances than primary producers on average which have a variety of life history strategies. As such, there might be even greater structure in species warming margins when functional groups are broken down into more explicit functional roles. This could explain why we observed a great deal of variation in thermal limits within each broad functional group (Fig. 2). However, variation in upper thermal limits between species might allow broad functional roles to be maintained within ecosystems as climates continue to warm (i.e. functional redundancy). However, global level functional redundancy has little relevance for local species loss (i.e. a species that provides a certain functional role will not help maintain ecosystem function in a local environment where that species is lost), and thus it is important to assess whether climate change vulnerability differs across regions and as species composition changes within functional groups.

We found that trends in functional group vulnerability within each broad-scale region somewhat reflected trends in vulnerability at the global scale (increasing vulnerability with increasing trophic level) (Supplementary Table 2). However, there was little variation between consumer species warming margins in the low-latitude region, potentially due to geographic sampling biases, where wet-tropical regions and developing nations tend to be under sampled compared to temperate regions (White et al., 2021) (Fig. 1). In the global analysis species warming margins were the narrowest in mid-latitude regions ($\sim 33^{\circ}$ absolute latitude), suggesting that mid-latitude species are the most vulnerable to climate warming, mirroring the findings of Hoffmann et al. (2013) on insects and reptiles. However, when we split low- and mid-latitude regions into two broad scale regions we found that primary producers and consumers are more vulnerable in tropical regions. Thus, vulnerability to climate change is likely to depend on a combination of the thermal environments species inhabit (e.g. tropical or temperate), the functional role they play in ecosystems, and their evolutionary histories. However, more data are required to make improved inferences on how functional group vulnerability changes across finer scale ecosystems and with different species compositions.

4.1. Study limitations

The main limitation of this study is not being able to account for plasticity or evolutionary potential in our analyses (Supplementary Information Section 4). Species are likely to be able to shift their thermal limits via plasticity or evolution, but a lack of data on the extent to which plasticity and evolutionary potential across species limits our capacity to factor evolution into vulnerability estimates. Nevertheless, the extent to which evolution is likely to shift upper thermal limits is likely to be small and unlikely to match the pace of climate warming (Gunderson and Stillman, 2015; Kellermann and van Heerwaarden, 2019). We also acknowledge that upper thermal limits are likely to under-estimate climate change vulnerability because rising temperatures will impose a range of sublethal effects on fitness at temperatures below species upper thermal limits (da Silva et al., 2020; van Heerwaarden and Sgrò, 2021). So while the absolute values of warming margins are unlikely to reflect the exact temperatures at which species will be negatively impacted by climate change, warming margins are still likely to capture an element of fitness/sub-lethal effects on phenotypes and hence the rank order of climate change vulnerability will remain (van Heerwaarden and Sgrò, 2021). Further research that seeks to examine plastic responses, evolutionary potential and sub-lethal effects of temperature on species abilities to perform functional roles will be important in improving estimates of functional group vulnerability. In addition, considering how variation in climate velocity (i.e. rate of climate change) across space is needed as not all regions are warming at the same rate (VanDerWal et al., 2013). Thus, species that have the same warming margins but inhabit regions with different climate velocity will differ in their vulnerability.

Finally, many groups of species are underrepresented in this analysis, we examined the warming margins of 1701 species which is well below the number of species that exist on the planet (estimates suggest between 5.3 million – 1 trillion (Locey and Lennon, 2016)) and contribute towards functional roles in the ecosystem. Thus, further studies that continue to estimate species thermal tolerances will be important for gaining a more robust understanding of how functional group vulnerabilities vary across the globe and finer scale ecosystems.

5. Conclusions

Our results suggest that global biodiversity loss due to climate change will possibly be non-random with respect to the function roles that species play in ecosystems. Species that contribute to higher trophic levels are likely to be the most vulnerable to further climate warming and primary producers are likely to be the most resilient to increases in environmental temperature. This trend of increasing vulnerability to climate change with trophic level is observed at the global scale as well as within broad scale tropical and temperate regions. Importantly, however, vulnerability trends might differ with changes in species composition across finer scale ecosystems, and thus caution should be used when transferring global vulnerability trends to local ecosystems. Overall, we observed variation in the climate change vulnerability of functional groups across all geographic scales, which is likely to disrupt functional group interactions and eventually impact ecosystem function (Voigt et al., 2003). Thus, governments and private organisations should seek to reduce carbon emissions to conserve ecosystem function for the future.

Ethics statement

N/A.

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CRediT authorship contribution statement

Conceptualisation: all authors.
Data curation: da Silva.
Formal analysis: da Silva.
Investigation: all authors.
Methodology: all authors.

Project administration: da Silva and Diamond.
Supervision: Diamond and Kellermann.
Validation: all authors.
Visualisation: da Silva.
Writing original draft: all authors.
Writing review: all authors

Data availability

Data is attached in supplementary material

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.161049.

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