Appendix 12: A comparative trait-based analysis of temperature sensitivity across a variety of taxonomic groups.

Abstract

In BICCO-Net I, we found that population response to climate change varied between species. Gaining an understanding of what drives this variation is important in order to predict future impacts of climate change. Here, we used long-term monitoring data to estimate variation in climate sensitivity across six taxonomic groups: birds, butterflies, moths, mammals, aphids and freshwater invertebrates. Climate sensitivity was measured as the proportional change in population abundance associated with a 1°C rise in temperature. We used a comparative trait-based approach to identify if certain character traits were associated with extreme responses to climate change. We found widespread variation in species responses to climate warming, with aphids, moths and butterflies tending to show a positive response to warming, while the mean response in the other taxa was not significantly different from zero. Results from our trait-analysis showed that temperature niche was positively associated with population response to climate warming in widespread species, and that widespread butterfly species showed a greater response to climate warming than rare butterfly species. These results can be explained by the positive association between ecological specialisation and range size, with widespread generalist species possessing a greater ability to adapt to environmental change than rare specialist species. Additionally, species with a warmer temperature niche are more likely to tolerate climate warming than species with a cooler climatic niche. Our models suggest that with the ongoing rise in global temperatures, proactive conservation effort should aim to protect rare species that prefer cooler conditions. However, given the low r^2 of our models the predictions should be carefully interpreted. Future research should aim to increase the level of variation explained in climate sensitivity, potentially by including a direct measure of ecological specialisation and dispersal ability that are comparable across multiple taxonomic groups.

Introduction

The impacts of climate change on biodiversity have been widely reported, with changes in species distributions and phenological shifts frequently used as evidence of species response to environmental change (Parmesan *et al.*, 1999; Hill *et al.*, 2002; Root *et al.*, 2003; Thomas *et al.*, 2004; Hickling *et al.*, 2006; Walther, 2010; Chen *et al.*, 2011; Bellard *et al.*, 2012). Fewer studies have examined population abundance changes in response to climate change, however evidence for this was found in BICCO-Net I and Appendix 5 of BICCO-Net II. A consistent theme across these studies is the widespread interspecific variation in response to environmental change, i.e. some species may benefit from climate change while others decline. A variety of studies have shown that variation in species response to environmental change can be partly explained by variation in species traits (Purvis *et al.*, 2000; Koh *et al.*, 2004; Pöyry *et al.*, 2009; Walker *et al.*, 2009; Murray *et al.*, 2010). For example, Angert *et al.* (2011) found variation bird and dragonfly range shifts were explained by diet breadth and egg laying habitat, respectively, while Chessman (2011) found variation in range shift of freshwater invertebrates was explained by thermal preference. This trait-based comparative approach has multiple benefits including the ability to make generalisations across multiple species and enabling predictions to be made regarding future biodiversity patterns (Fisher & Owens, 2004).

Currently comparative studies have tended to focus on explaining variation in range shift, change in range size and extinction risk. Here, we further this field by using the trait-based comparative approach to explain the variation in population abundance changes in response to climate warming. Additionally, we add to the taxonomic scope of such research by including the less-well studied freshwater invertebrates, moths, aphids and mammals alongside the more commonly studied bird and butterfly fauna.

In this study, we examined a range of key traits that were expected to influence a species response to climate warming. First, we included climatic niche, which has been shown to be an important determinant of a species ability to respond to climate change, with lower thermal tolerance associated with declines due to the reduced tolerance of warmer conditions (Jiguet *et al.*, 2006; Devictor *et al.*, 2008). Alongside a measure of species temperature niche, we also included precipitation niche, as rainfall was associated with population changes for a number of species (particularly moths) in BICCO-Net II, Appendix 4: A cross-taxa appraisal of the impact of climate change on species' population size. Rarity is often used as a surrogate for a number of species characteristics, but particularly for ecological specialism, with rarer species likely to be more specialised (Garcia-Barros & Benito, 2010; Angert *et al.*, 2011). The ability of widespread species to switch habitat or food resources means they have a greater ability to adapt to novel conditions during times of environmental change. We therefore predict that widespread species will show a greater positive response to climate warming than rare species. Ectothemic species have a greater reliance on external temperatures than endotherms and are therefore more susceptible to climatic pressures. Devictor *et al.* (2012) found that butterflies tended to show a greater response to climate change than birds and attributed this in part to differences between in the thermoregulatory processes of the taxa. We predict that we will find support for Divictor *et al.* (2012), with results that shows ectotherms had a stronger population response to climate change than the endotherms. Concerns have been raised regarding trophic mismatches occurring as a result of distributional and phenological changes in response to climate change (Edwards & Richardson, 2004; Schweiger *et al.*, 2008; Thackeray *et al.*, 2010). Schweiger *et al.* (2012) used species distribution models to highlight potential range mismatches for butterfly species and their host plants, while Edwards & Richardson, (2004) discovered potentially devastating levels of phenological decoupling between trophic levels and functional groups of the pelagic community of the north sea. We aim to add to this research by testing if species population response to climate warming varies between trophic levels. The final trait we consider is a comparison of the population response between freshwater and terrestrial organisms, evidence suggests that both communities have respond to climate change but a direct comparison between groups remains untested.

Current conservation effort tends to be reactive, i.e. species X has declined therefore we should take action Y to restore/rescue the population. However, many have argued that switching to a proactive approach to conservation will lead to greater efficacy of conservation effort (Drechsler *et al.*, 2011). Prediction is a valuable tool for the proactive conservation approach, whether that be in terms of predicting future distribution patterns or future responses to likely environmental scenarios. In this study we produce two sets of predictions which will be of value to conservation practitioners. Firstly, we predict a proportional change in population size in response to 1 degree rise in temperature. Secondly, the parameter estimates of the comparative trait models enable us to predict species response to climate warming given their inherent trait characteristics.

Methods

Climate sensitivity

Abundance data were extracted for butterflies, birds, moths, mammals, aphids and freshwater invertebrates from various long-term monitoring schemes (Table 1). Each scheme used standardised survey methods to collect species abundance data from multiple sites across Britain. The time frame and number of survey sites varied between groups (Table 1). For each species, we estimated climate sensitivity as the proportional change in abundance associated with a 1°C rise in temperature. First, we extracted the fitted value for the final year of the species time-series (fitted) from the national-scale time-series climate models (details in Appendix 4). We then used the same species specific national-scale model to predict abundance in the final year but added 1°C to the temperature value (predicted). Climate sensitivity was then estimated for the species as the percentage difference between the fitted and predicted value. This measure of climate sensitivity was used as the response variable in the phylogenetically informed comparative analyses described below.

Traits

In this study, we focussed on broad trait characteristics to ensure they were comparable across the wide range of taxonomic groups.   We first calculated three traits, rarity and the two climate indices (temperature and precipitation), using the using the survey data. Rarity was calculated as the proportion of survey sites that a species occupied during the survey period, given all sites surveyed for the taxonomic group in question. The climate indices were estimated from gridded 5 x 5 km, monthly mean temperature and rainfall data taken from the Met Office UKCP09 datasets (http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/monthly/gridd ed_monthly.html - Perry & Hollis 2005). First, for each survey site, we identified the mean annual temperature and rainfall between 1970 and 2010. Then, for each species, we estimated the mean temperature and rainfall across all occupied sites. To ensure the two climate indices were comparable across the taxonomic groups and not biased by the spatial variation in site locations, we subtracted the respective mean climate variable across all sites surveyed for the taxonomic group from the species mean climate score. Therefore, our climate indices essentially placed species on a gradient from warm to cold, and wet to dry species given the available climate space of the site locations for the taxonomic group. As these traits were estimated from the survey data were able to ensure they were comparable across the different taxonomic groups.

In addition to the survey based traits, we classified species based on trophic level. Given the taxonomic scope of this study, this trait was included as a binary variable with species grouped as primary or secondary consumers. The very few species included in our analysis that could be considered tertiary consumers (e.g. sparrow hawk) were grouped in with the secondary consumers. We included a binary trait that classified species as either ecto- or endotherms. Finally, we included a binary variable that distinguished purely freshwater taxa from those that are completely or partially terrestrial.

Analysis

We used the '*pgls*' function of the R package '*caper*' to run phylogenetically informed trait-based comparative analysis to examine correlates of climate sensitivity. First, we ran models separately for each taxonomic group to examine the group level correlates of temperature sensitivity. Temperature index, rarity and trophic level (where there was sufficient inter-specific variation), were included as predictors in these models. We excluded the rainfall index from all analysis as it was strongly negatively associated with the temperature index (r = 0.88), however it remains important to the discussion regarding the temperature index results. We also modelled temperature sensitivity across all taxa in a single model, and as with the group specific models we included, temperature index, rarity and trophic level as predictors. In addition to these traits we also included the binary traits for terrestrial vs freshwater and endo- vs ectothermic lifestyle. In all models, we tested for significant interaction terms and curved relationships (using quadratic terms).

Phylogeny

Due to the lack of available genetic information for many species used in this study, we built a phylogeny based on taxonomy.   We used the '*as.phylo*' function from the R package '*ape*', to convert the taxonomy into a phylogeny with branch lengths set to one and polytomies at each node. The taxonomic levels, Kingdom, Phylum, Class, Order, Family, Genus and Species were used as nodes for this phylogeny.

Results

We found widespread variation in species predicted response to a one degree rise in temperature (Figure 1). Aphids, moths and butterflies had positive mean temperature sensitivity scores that were significantly different from zero, while mammals were the only taxa to have a negative mean sensitivity score. A positive mean sensitivity score suggests that on average an individual from these groups (particularly aphids and moths) are likely to benefit from a one degree rise in temperature. In contrast, taxa with a negative mean sensitivity score are likely to suffer losses following a one degree rise in temperature.

We discovered that the significance and direction of the trait-trend relationships varied between taxa. Rarity was significantly positively associated with temperature sensitivity in the butterfly trait model (Table 2b). This result suggests that widespread butterfly species are likely to benefit from a one degree rise in temperature, while rare, localised species are likely to decline. We discovered a significant interaction between rarity and temperature index in the trait-based model for moths (Table 2c). This significant interaction shows that the positive influence temperature index on temperature sensitivity declines as species become rare, and is plotted in figure 2. The final significant trait relationship in the single taxa models was the negative relationship between temperature index and temperature sensitivity in the freshwater invertebrates (table 2e). Here, our model appears to show that species which prefer/currently occupy warmer conditions are likely to decline with a one degree rise in temperature, compared to those species with a cooler temperature

index. Trophic level was non-significant on all occasions where it was included as a predictor (i.e. the models for birds, mammals and freshwater invertebrates).

We included terrestrial stage and thermoregulation process alongside rarity, temperature index and trophic level in the trait-based model covering all taxa. After dropping non-significant terms from the model, only temperature index, rarity and the two-way interaction between them were retained in the model. The addition of the non-significant variables and their associated interaction terms provided no improvement on model performance based on AIC. We therefore only present results from the simple model (Table 3 - $DF = 539$, $F = 7.94$, $SE = 19.54$, $p < 0.001$, $r^2 = 0.04$, $\lambda = 0.428$). The significant interaction between temperature index and rarity in our multiple taxonomic group model closely matches the pattern seen in the moth model. We found the relationship between temperature index and temperature sensitivity is positive for widespread species, but the relationship begins to flatten with the rarer species (Figure 3). This suggests that a warmer temperature index is important for widespread species to prosper with climate warming, while other factors are more important for driving the response of rare species to an increase in environmental temperature. As moths make up a large proportion (48%) of the total number of species included in the multi-taxa analysis it is unsurprising that the multi-taxa model shares similarities with moth model.

In general, our models explained a low amount of variation in temperature sensitivity.   The models for birds and mammals had an r^2 of < 0.001, while the highest r^2 at 0.1 was discovered for trait-based model for moths.

Discussion

Using our estimate of species' temperature sensitivity scores we show that aphids and moths and, to a lesser extent, butterflies are predicted to benefit from a one degree rise in temperature. At first glance this result may appear to be good news regarding the conservation of species in the face of climate change. However, our models did not account for the impact of several other factors that are likely to limit any potential population expansions. One such factor is habitat availability: populations will not be able to expand if they reach the limit of their carrying capacity and lack suitable habitat to move into. Additionally, potential trophic mismatches, or the breakdown of interspecific interactions that may be critical to a species ability to persist and were not covered by the predictions. The mean response of all other taxa was not significantly different form zero, suggesting that species within these groups were just as likely to decline in response to climate warming as increase. Our models support the findings of Appendix 3 of BICCO-Net II, where aphids were shown to have benefitted from climate change, and inconsistent responses were discovered for the majority of the other taxa. In contrast, moths were particularly negatively affected by climate change in Appendix 3, whereas our models predict moths to increase in response to climate warming. A possible reason for this discrepancy is that our predictions were not a complete measure of future climate impacts as they were based solely on an increase in temperature. The difference could then be signalling that the negative impact of climate change on moths in Appendix 3 could be due to precipitation.

A key result of this study was the significant interaction between rarity and temperature index in explaining variation in species response to climate warming. This result was significant in the model for all taxa but was likely driven by its importance for moths, which contribute 48% of the species in this study. Figures 2 and 3, illustrate that the positive relationship between temperature index and temperature sensitivity gradually flattens as species become increasingly rare. We hypothesised that temperature index (our measure of a species temperature niche) would be positively correlated with species response to climate warming, as species with a warmer climatic niche have an increased tolerance for warm conditions (Jiguet et al., 2006; Devictor et al., 2008). Our results partly support our hypothesis, with a positive association between temperature index and response to climate warming detected in widespread species. The lack of a correlation between temperature index and response to climate warming for rare species could be due to the link between rarity and ecological specialism. As mentioned in the introduction, rarity is often used as a surrogate for ecological specialism, with specialists more likely to be rare (Garcia-Barros & Benito, 2010; Angert et al., 2011). We believe the significant interaction reflects the ability of widespread generalists (that prefer warm conditions) to adapt and take advantage of a warmer climate by occupying newly available resources, in contrast to the rare specialist species remain restricted by habitat or food resources and therefore regardless of the temperature niche they do not benefit from a warmer climate. We believe the significant positive relationship between rarity and response to climate warming in butterflies reflects that greater ability of generalists to adapt to novel environmental conditions than specialists.

Finally, the negative relationship between species climate niche and response to climate warming was contrary to our hypothesis, and was also in contrast to the results in Appendix 9. We believe that this result is due to differences in the techniques used to estimate species temperature niche. Some freshwater species are eurytherms (i.e. can function in any temperatures) so their spatial location may not represent their climatic niche. This was accounted for in the thermal tolerance measure of Appendix 9, but not in the method we used to estimate of a species temperature niche. To highlight this *Diura bicaudata*, is a eurytherm, so it can tolerate high temperatures and is classified as such in Appendix 9, however in our analysis it is the species with the coolest temperature niche. An area for future work would be to establish a technique to estimate species thermal tolerance that incorporates information from a variety of sources, but is remains comparable across taxonomic groups.

With the continued rise in greenhouse gas emissions, the impact of climate change is likely to intensify (IPCC, 2013). As a consequence of this, our models suggest that small ranged species that occupy cooler regions should be prioritised for targeted proactive conservation effort. However, our models had low r^2 and therefore the predictions produced will likely suffer from low accuracy. An area for future research would be to aim at improving the level of variation in temperature sensitivity explained by the trait-based models. A potential solution for this would be to include direct measures of habitat specialism and dispersal ability rather than using rarity as a broad over-arching surrogate variable. Evidence suggests that both habitat specialism and dispersal ability are likely to influence species response to climate change and therefore are likely to improve our models (Pöyry et al., 2009). Despite the low r^2, our recommendation for proactive conservation finds support through other studies that have shown similar trait relationships based on different response variables, such as extinction risk and range shift (Purvis et al., 2000; Manne & Pimm, 2001; Warren et al., 2001; Cardillo et al., 2008).

In conclusion, we found widespread variation in species predicted response to a one degree rise in temperature, and that aphids, moths and butterflies tend to respond more positively than other taxa. We found that rare species that prefer cooler climates are most threatened by climate warming and encourage proactive conservation effort in order to protect these species with the ever increasing threat of climate change.

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Table 1 Details of surveys used to produce yearly species indices

Taxonomic group	Site number	No. species	Survey years	Source
Terrestrial mammals	~3000	6	1995 – 2011	http://www.bto.org/volunteer-surveys/bbs
Bats	~1200	7	1998 – 2011	http://www.bats.org.uk/pages/nbmp.html
Birds	~3000	84	1966 – 2011	http://www.bto.org/volunteer-surveys/bbs
Butterflies	1424	51	1976 – 2011	http://www.ukbms.org
Moths	13	263	1975 – 2010	http://www.rothamsted.ac.uk/insect-survey/
Aphids	12	75	1970 – 2010	http://www.rothamsted.ac.uk/insect-survey/
Freshwater Inverts.	1463	57	1983 – 2007	EA & SEPA (see appendix 9 for full citation)

Table 2 The parameter estimates for the trait models that explained variation in temperature sensitivity for each taxonomic group. Aphids were excluded from the single taxa models due to a lack of interspecific variation in the chosen traits. The overall model coefficients are shown alongside the name of each group. For the estimated level of phylogenetic signal (λ) in each model, we use asterisks to highlight those that were significantly different from 0 (the value before the comma) and 1 (after), * = p <0.05, ** = p <0.01, *** = p <0.001.

Parameter	Estimate	SE	t	p
a) Birds - DF=80, F=0.07, SE=4.36, p=0.98, r^2<0.001, λ=0 (ns,***)				
Intercept	1.40	2.75	0.51	0.613
Rarity	-0.14	2.69	-0.05	0.958
Temp. index	1.35	4.10	0.33	0.743
Trophic - Sec. Cons.	-0.69	2.47	-0.28	0.783
b) Butterfly - DF=48, F=3.15, SE=5.67, p=0.05, r^2=0.08, λ =0 (ns,**)				
Intercept	-0.98	1.89	-0.52	0.605
Rarity	8.03	3.67	2.19	0.033
Temp. index	3.44	3.31	1.04	0.304
c) Moth - DF=259, F=10.74, SE=21.35, P<0.001, r^2=0.1, λ =0.29 (**,***)				
Intercept	32.64	12.75	2.56	0.011
Temp. index	-251.91	82.15	-3.07	0.002
Rarity	-16.85	13.13	-1.28	0.201
Temp. index : Rarity	550.11	130.30	4.22	<0.001
d) Mammal - DF=9, F=0.68, SE=6.12, p=0.59, r^2<0.001, λ =0.64 (ns,ns)				
Intercept	0.88	7.95	0.11	0.914
Rarity	-12.37	11.29	-1.10	0.302
Temp. index	5.86	10.13	0.58	0.577
Trophic - Sec. Cons.	0.06	6.31	0.01	0.993
e) Freshwater invert. - DF=53, F=2.9, SE=32.6, p=0.04, r^2=0.10, λ =0 (ns,***)				

Intercept	15.57	16.17	0.96	0.340
Rarity	83.36	71.09	1.17	0.246
Temp. index	-22.49	12.33	-1.82	0.074
Trophic - Sec. Cons.	-15.33	18.17	-0.84	0.403

Table 3 The parameter estimates for the model that best explained variation in temperature sensitivity across all taxonomic groups.

Parameter	Std. estimate	Std. error	T	P
Intercept	10.51	8.63	1.22	0.224
Temp. index	-28.26	6.52	-4.34	<0.001
Rarity	5.10	7.19	0.71	0.478
Temp. index : Rarity	145.13	38.54	3.77	<0.001

Figure 1 The mean temperature sensitivity for each group included in the analysis. The standard error of the mean are plotted with asterisks added to highlight those mean estimates that are significantly different from zero (* = p <0.05, ** = p < 0.01, *** = p < 0.001).
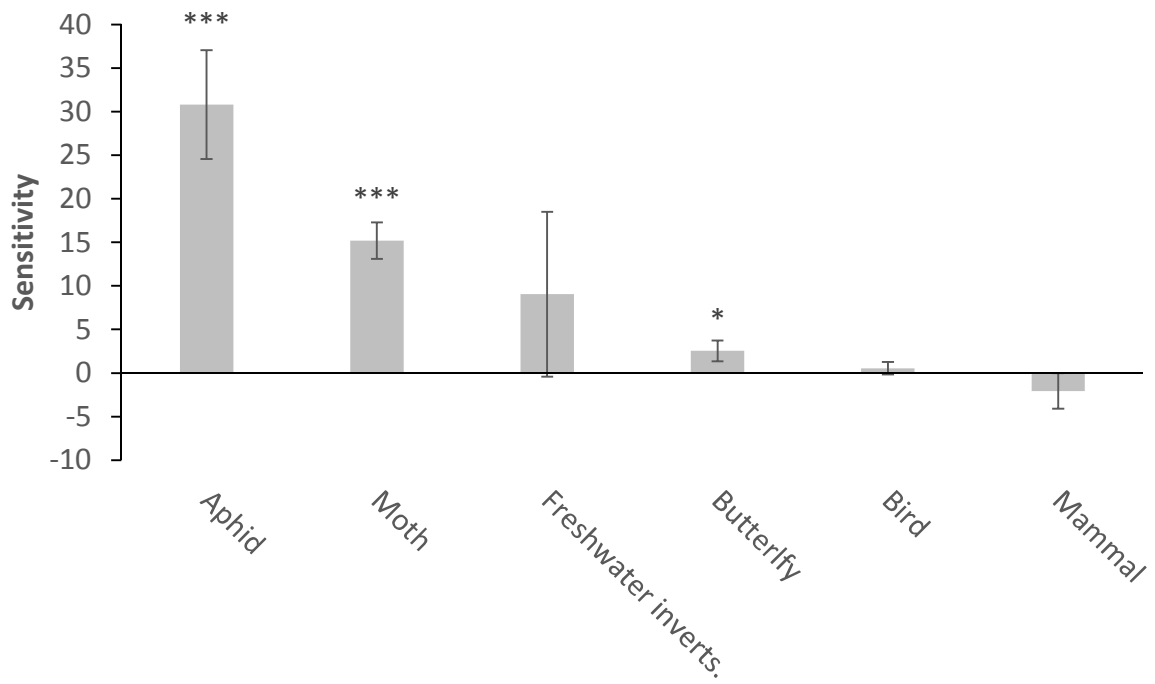
Figure 2 An interaction plot showing how the relationship between temperature index and sensitivity to temperature varies with rarity for moths.
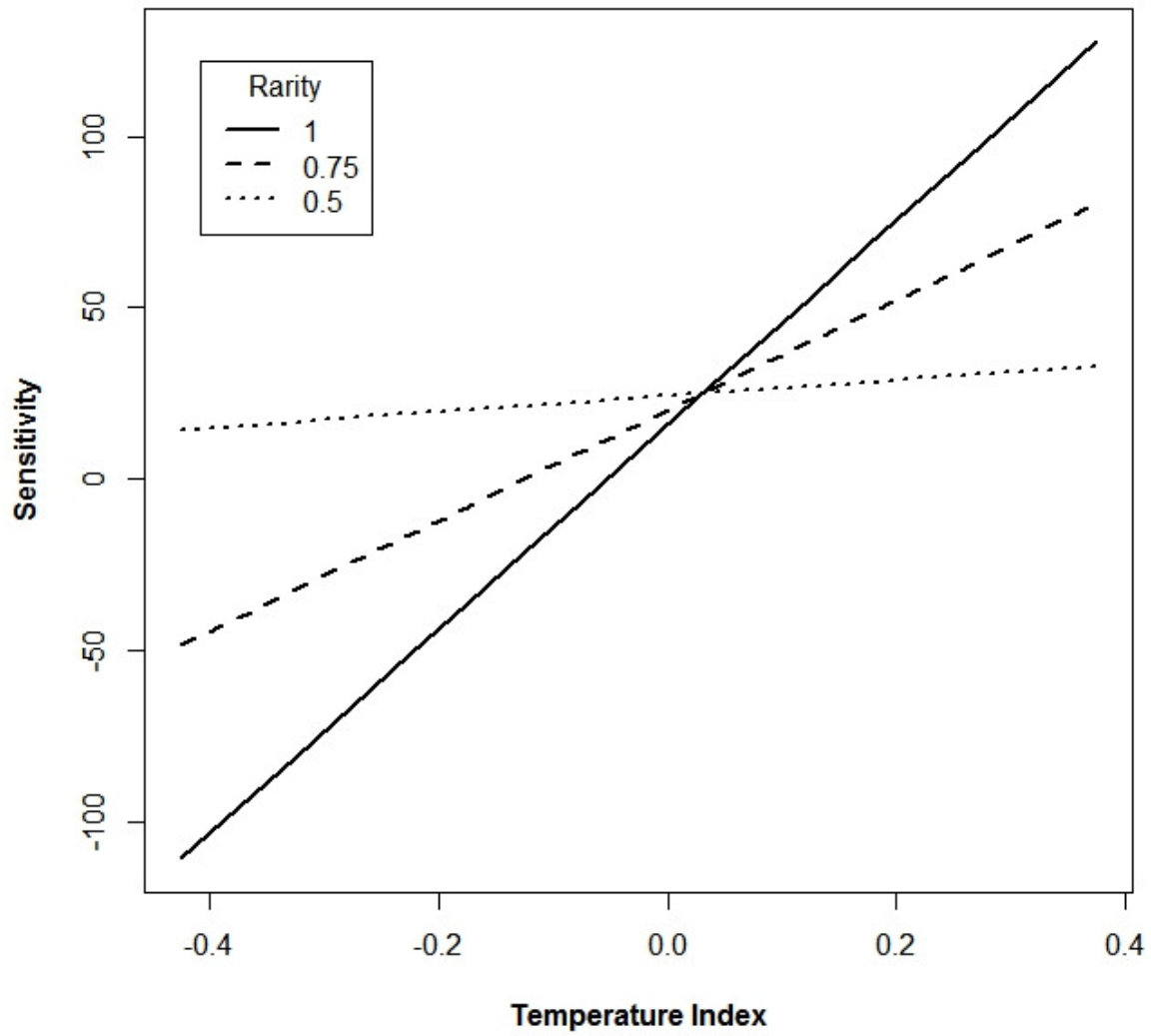
Figure 3 A plot showing the significant interaction between temperature index and rarity for explaining variation in temperature sensitivity across all taxa.