EXPLAINABLE HETEROGENEITY? A META-ANALYSIS OF ARCTIC AND SUBARCTIC RESPONSES TO CLIMATE CHANGE

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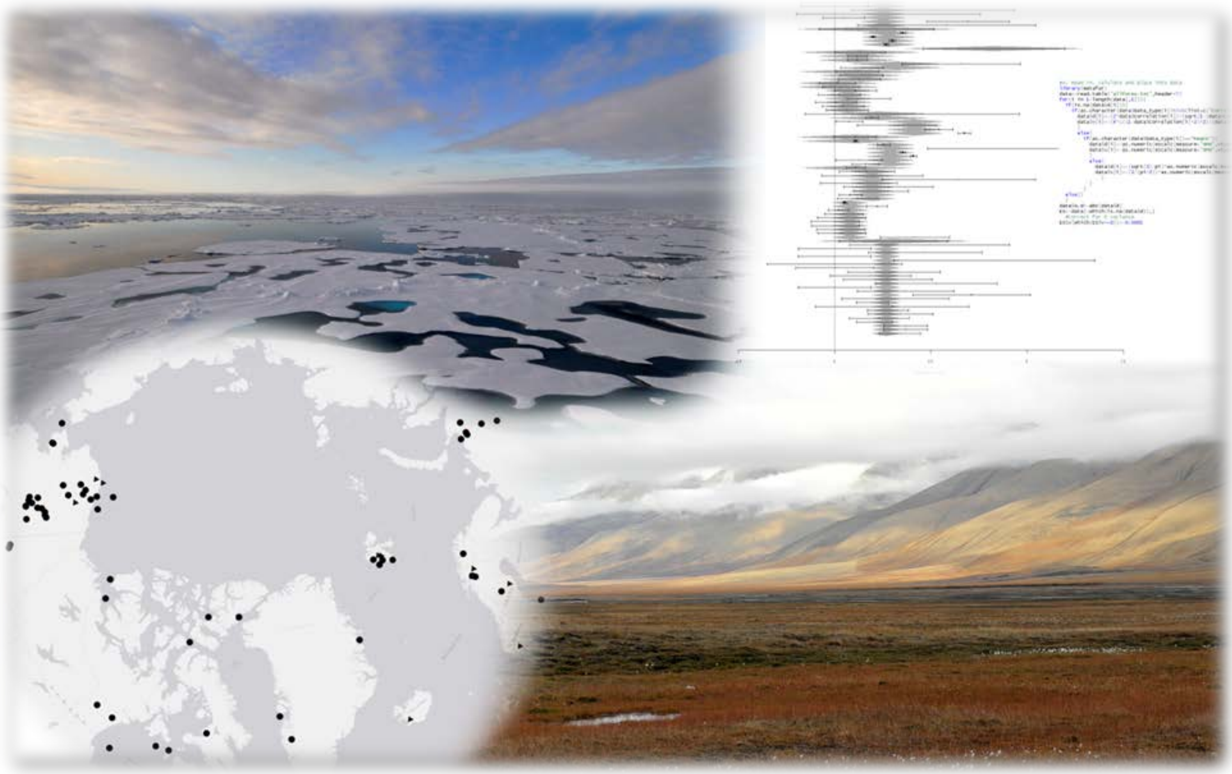

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ABSTRACT

Species may respond to climate change in a number of ways (Walther *et al.* 2002) and broad meta-analyses suggests that these responses are occurring globally (Parmesan & Yohe 2003). The way that species respond will have a substantial effect on their survival and the maintenance of regional community assemblages. Distributional responses, for example, are limited by geographic and topographic constraints, and where the ranges of suitable habitat become constricted, species loss may result (Thomas *et al.* 2004). Thus it is important for conservation planning to be able to predict these responses: however, there is considerable uncertainty in predictions due to substantial heterogeneity in species responses. This study focuses on observed species responses in the arctic and subarctic regions, and uses meta-analysis to explore drivers of heterogeneity in responses. While the results show that species are clearly responding to climatic change in the arctic, there is also considerable heterogeneity in the magnitude of these responses. Methodological and other study-level variation account for much of this heterogeneity, while effects of ecological factors were idiosyncratic: spatial location and degree of climate change had no significant effect, and there were only a few trends in the dataset that were explained by habitat or taxonomic factors. Substantial heterogeneity was unexplainable with the collected data, and while there are limitations of the current literature, this may have negative implications for the predictability of future species responses.

CONTENTS

INTRODUCTION

Regional climatic changes, together with the global mean increase in temperature, are affecting natural systems across the globe. Species and ecosystems have adapted to altering climate throughout evolutionary history, but the current rate of change is greater than that observed in any previous time period (IPCC 2007). Changes in climate are predicted to have several effects on species (Walther *et al.* 2002), namely:

1. Shifts in the distribution of a species or species group, either latitudinally or altitudinally, in order to remain within climatic tolerances.
2. Changes in the density of a species or species group in a specific location.
3. Changes in the phenology of a species, such as in flowering, egg laying or migration
4. Alterations in individual characteristics including morphology (such as body size) or behaviour.
5. Shifts in genetic frequencies.

Several high-profile meta-analyses have documented that responses of these types have already occurred globally. Root *et al.* (2003) found that in reports of the above effects on species or species groups, more than 80% were in the direction predicted if climate change was the cause. This general finding is corroborated by Parmesan and Yohe (2003) and Rosenzweig *et al.* (2008).

The possible responses of species to climate change are predicted to have a substantial effect on the survival of species and on regional biodiversity. Shifting distribution is only possible if suitable habitat is available to disperse into, but habitat destruction and geographic/topographic constraints may prevent this (Svenning & Skov 2007). A substantial level of species loss may result from constricted distribution (Thomas *et al.* 2004) or loss of beneficial interactions as ranges of interacting species diverge. Changes in phenology may lead to trophic mismatch between interacting species, and thus declines through loss of feeding opportunities or mutualisms (Van der Putten *et al.* 2010). These are just some of the ways in which climate change is likely to affect species survival, and it is important for conservation planning to be able to predict these effects.

Modelling techniques are increasingly being used to predict species responses to future climate change, based on information such as distribution or physiological tolerance. However, there is a large degree of uncertainty in these predictions: models depend on accurate and complete distributional or physiological data, often don't take into account species interactions or adaptation (Davis *et al.* 1998; Dormann 2007), are limited by the climatic variables chosen and uncertainty in future climate (Pearson & Dawson 2003), and neglect lags, thresholds and non-linearity in responses of species to climate forcing (Wischnewski *et al.* 2011). These problems demonstrate that the current, and thus future, occurrence and distribution of a species is not only related to abiotic conditions, but is also affected by changes in adaptive or phenotypically plastic tolerances to these abiotic conditions, changing multispecies interactions, and/or dispersal ability.

While work is being done to create frameworks for building species interactions into predictive models (Berg *et al.* 2010), there is an enormous degree of complexity in the interactions and other factors that limit species survival in given locations (Walther 2010). This complexity limits both the precision and potential realism of models, and requires further work characterising the properties of species and their habitats that drive this uncertainty. A prediction-validation approach to this problem would require both a large degree of modelling effort in order to forecast the effects of a wide range of variations under a range of climatic scenarios, as well as considerable time for the predicted interval to occur for validation. However, by studying reported responses of species to climate change that have already occurred, especially those with heterogeneous results, it may be possible to identify factors confounding current predictions of future responses (Post *et al.* 2009b).

The arctic may be a useful system within which to examine this area. Carrying out such an analysis on a global scale would require an enormous data collection effort, encompassing a large variety of ecosystems. The arctic and subarctic region has undergone warming at two to three times the rate of the rest of the planet (IPCC 2007), stimulating considerable research into the responses of species to this warming (reviews by Post *et al.* 2009b; Wassmann *et al.* 2011). Heterogeneity in species and ecosystem responses has been reported, and these responses vary both spatially and temporally. The harsh environmental conditions in the Arctic induce considerable limitations on species establishment and ecosystem complexity (Wookey *et al.* 2009), providing two-fold benefits for this study: the responses of species to climate change, both simulated and real, are likely to become more evident as these limitations are reduced, and responses may be less likely to be obscured by a complex web of unknowable interactions (Doak *et al.* 2008; Van der Putten *et al.* 2010).

The arctic is also the study location for a large number of experiments imposing simulated climate change on ecosystems (see Elmendorf *et al.* 2012), including the International Tundra Experiment (ITEX) (Henry & Molau 1997). This long-term research project employs standardised passive warming chambers and other methods to simulate temperature increases (approx. 2°C) and other abiotic changes that are predicted to occur by the year 2050 (Marion *et al.* 1997; ACIA 2004). Elmendorf *et al.* (2012) recently reported a meta-analysis of the results from ITEX and other warming experiments in the arctic, which found significant levels of heterogeneity in responses to imposed changes both between species responding to the same climatic change and within species responding to different climatic changes. It remains to be seen whether induced responses accurately reflect responses to actual climate change, and how heterogeneity varies between these results.

KEY QUESTIONS

- Is there systematic, quantifiable evidence for ecological changes in arctic populations across the taxonomic spectrum, and are these attributable to climate change?
- To what degree is there heterogeneity in these responses?
- Do the direction and magnitude of observed responses and their heterogeneity agree with the findings of experimental studies?
- What factors influence the direction and magnitude of responses, and hence explain this heterogeneity?
- Therefore, to what degree is it possible to explain the responses of ecological systems to climate change, and how much heterogeneity is left unexplained?

METHODS

In view of the publication of Elmendorf *et al.* (2012) during literature collation and data collection for this study, the focus of data collection was shifted towards observed responses to climate change. Requests for the data used by Elmendorf were rejected due to future planned publications. Data was collected for a sample of experimental studies for comparison with the data from observational studies, and findings will also be compared with those reported by Elmendorf.

DATA COMPILATION

A database of relevant literature was collated to provide meta-analysis data. This dataset consisted of studies reporting an observed or induced response to climate change in the arctic or subarctic, and was judged against a strict set of criteria (see Appendix I: Extended Methods).

Response data from papers fulfilling the criteria were entered into a meta-analysis database along with other relevant data, described in Table 1. Response data consisted of several different types of measures, and where presented in graph form data was extracted using Engauge (Mitchell 2009). All papers that did not report latitude/longitude in the text provided maps of the study site, from which coordinates were estimated using iTouchMap (2012). Taxonomic data and guild categories were compiled from researching species in the Integrated Taxonomic Information System (2012)

Many studies included responses from multiple regions or of multiple different taxa: where these data were independent, they were included separately.

EFFECT SIZE CALCULATIONS

Effect sizes render factor levels comparable despite the fundamentally different scale that different response types are measured on (biomass, range size, etc). An effect size and weighted standard error for each independent response was calculated for different types of data (see Table 3). In order to permit comparison between studies, effect sizes were converted to the standardised mean difference, selected because this effect size includes a correction factor that removes biases due to small sample sizes.

The sign of each effect size varied depending on the metrics used in the study, so these were standardised to ensure valid comparisons with respect to increasing temperature/time (Table 2); for example, Regehr *et al.* (2007) reported a positive relationship between survival probability of polar bears (*Ursus maritimus*) and sea ice breakup date, but breakup date is negatively related to temperature and year, so the sign of this effect was reversed.

Table 1: Categories of associated variables collected for each reported response

Category	Variable	Levels/units	Notes
Structural	Study	Unique ID for each study	
	Study type	Observation or Experimental	
	Type of climatic change	Time or Temperature	Control for inherent differences between studies using these metrics
	Sampling dates	Years sampling started and ended	Control for change in climatic change over time
	Data type	Correlation, Regression, Rate, Means, Proportions.	See Table 3
	Response type	Population density/size, Range, Species richness, Physiology	
Extrinsic	Latitude and Longitude	Decimal degrees	Centre point taken of larger study areas
	Study Biome	Terrestrial, Marine, Freshwater, Land-breeding marine	
	Degree of climatic change	Years or °C	See above
	Region, country, location of study	(Many)	
	Habitat type	Forest, Heath, Cliffs, Tundra, Multiple habitats, Dry heath, Fellfield, Bog, Treeline, Freshwater, Snow slope, Mountainous treeline, Snow/ice, Sea	
Intrinsic	Taxonomic data	Full taxonomic classification data	
	Guild data	Three nested categories	

Table 2: Interpretation of sign direction for each response type

Response type	Positive effect size	Negative effect size
Population density or size	Increasing	Decreasing
Latitudinal range boundary	Extending northward	Extending southward
Longitudinal range boundary	Extending eastward	Extending westward
Range size	Expanding	Contracting
Physiological parameters	Increasing	Decreasing
Phenology	Earlier	Later

Table 3: Details of the calculation of effect sizes and their sampling variances.

Data type	Intermediate effect size(s) and variance(s)	Converted effect size	Method
Means	Unstandardised mean difference, Cohen's *d*, and weighted variance	Standardised mean difference, Hedge's *g** and weighted unbiased[i] standard error (Hedges & Olkin 1985)	Function escalc in metafor (Viechtbauer 2010)
Correlations	Raw correlation coefficient and weighted variance		Manual implementation of formulae described in Borenstein *et al.* (2009)
Slopes from regression/ rate data	Converted to correlation coefficient and weighted variance		Manual implementation of formulae described in DeCoster (2004) and Borenstein *et al.* (2009)
Proportions	Converted to log odds ratio and weighted variance		Function escalc in metafor (Viechtbauer 2010), manual implementation of formula in Borenstein *et al.* (2009)
Any of above, but with only F value & n usable	N/A		Online calculator (Lipsey & Wilson 2001; Wilson 2012)
Any of above, but without sufficient data	Discarded		

Positive and negative effect sizes are treated by analysis as opposing responses, but both demonstrate a response to climate change. To account for this, absolute values of the effect sizes were calculated in order to analyse solely the magnitude of responses.

META-ANALYSES

Meta-analysis modelling and associated functions were carried out using the metafor 1.6-0 package (Viechtbauer 2010) in R 2.14.1 (R Development Core Team 2011). Metafor is currently the only available R meta-analysis package capable of fitting mixed-effects models with multiple categorical and/or continuous moderators (explanatory variables) (Viechtbauer 2010), although it is not yet capable of fitting models with moderators that are not fully crossed[ii]. Stand-alone meta-analysis programs are available, but either do not have the capabilities of metafor, are too expensive, or were otherwise unavailable.

SUMMARY MODELLING

Linear fixed-effects intercept-only models using weighted[iii] least squares were used to estimate overall summary effect sizes using the both absolute and directional calculated effect sizes and corresponding sampling variances. These were fitted to the observational and experimental datasets separately to quantify and test significance of responses of species to observed and induced climatic change. The z-value, significance and SE of the summary effect size, and an estimate of the residual heterogeneity (QE-/QH-value, test statistic for unexplained variation between effect sizes) and its significance were all computed.

As publication bias is a major criticism of meta-analyses, fail-safe calculations were run for the two datasets using the Rosenberg method, selected because it is the only method that takes account of weighting of effect sizes (Rosenberg 2005). Given the a set of effect sizes, these estimate the number of additional hypothetical effect sizes averaging null results required to reduce the significance level of the weighted summary effect size to a particular value, in this case p=0.05.

MODERATOR MODELLING

To study the effect of different explanatory variables (moderators), mixed-effects models were fitted using the restricted maximum likelihood estimator of the estimate of total heterogeneity (τ^2), in order to explore the degree to which variation in responses can be explained by the data collected (Table 1). In metafor, all fitted moderators are treated as random effects in calculating the variance of the summary effect size variance, while also treated as fixed effects in order to compute their effect on the response of interest and the significance of this effect. Stepwise model selection from a fully saturated model was not possible because it is unfeasible within the current implementation of metafor to fit categorical moderators which are not fully crossed. Therefore each moderator was tested individually for significance in explaining heterogeneity in effect size by a test of moderators (QM-value, test statistic vs. H_0: effect of all moderators equals 0) and comparisons of significance between each moderator's estimated difference from the summary effect size (z-test). Where a moderator was found to be important, this was included in further levels of model building in order to achieve an approximation of a minimal adequate model.

To guide this approach to model fitting, explanatory variables were separated into three categories before analysis according to the magnitude of their assumed impact on heterogeneity in responses. This was prompted by examination of other ecological meta-analyses (Arft *et al.* 1999; Rustad *et al.* 2001; Dormann & Woodin 2002; Newsham & Robinson 2009), in order to sequentially take account of possible confounding variables at the study- or regional-level before examining variation at the species level. In order of greatest impact, these categories were: structural effects, extrinsic effects, and intrinsic effects, shown in Table 1. Broadly, structural effects are those that are properties of the study, extrinsic effects are those that broadly describe the possible abiotic influences on a study population, and intrinsic effects are those that describe biotic influences.

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[i] The standard error is referred to as unbiased because it is weighted by the sample size of the statistics used to calculate the corresponding effect size estimate (in this case, standardised mean difference). See Hedges and Olkin (1985)

[ii] Two categorical factors are fully crossed when every possible pair-wise combination of levels of the two factors is included in the dataset corresponding with values of the response variable. Where fully crossing variables in not possible (i.e. not every study included every habitat or every species), nesting is generally used, but this is not possible in the current implementation of metafor.

[iii] Weighted by the precision of the effect size estimate (the unbiased standard error, see note i

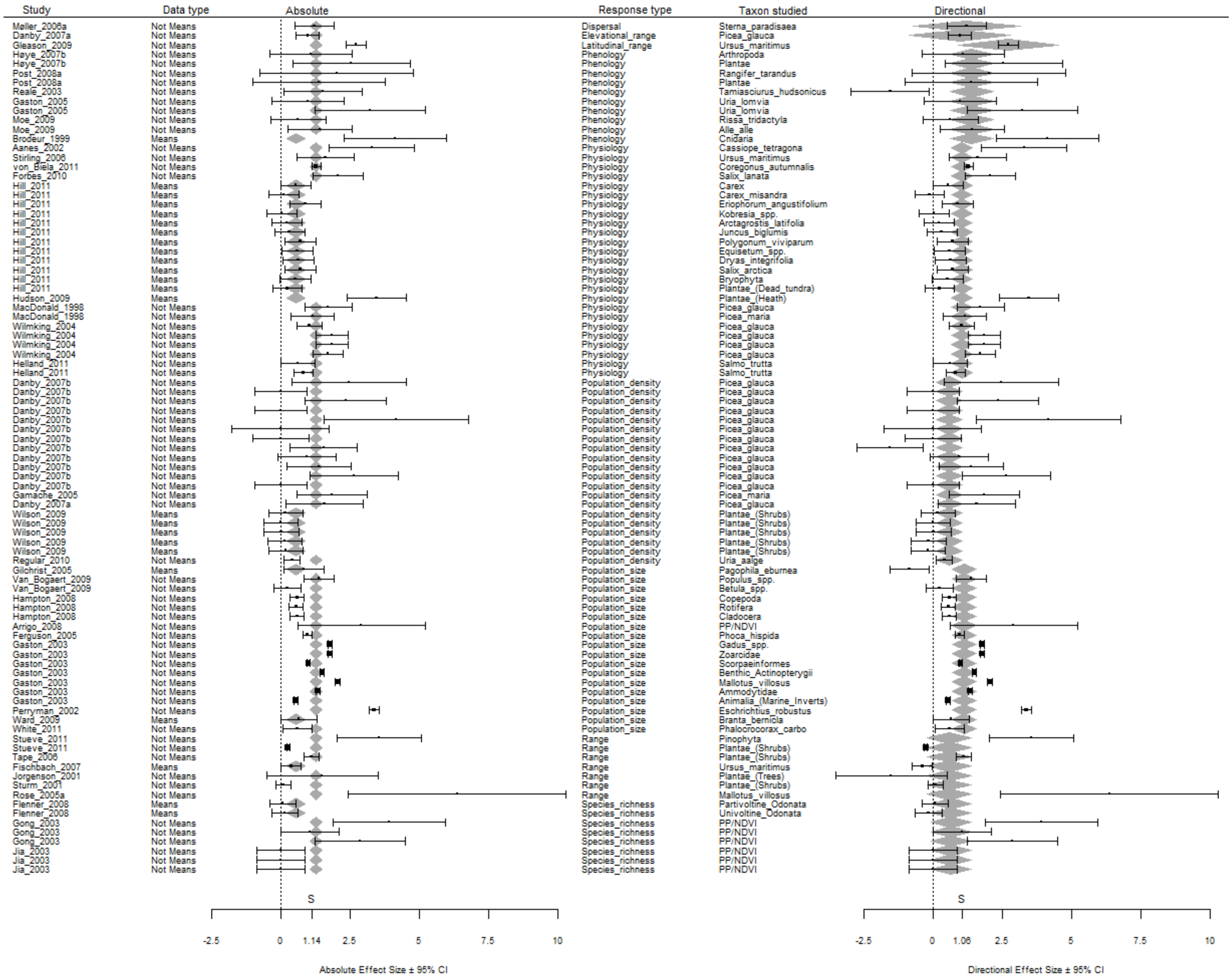


Figure 1: Summary ecological responses to climate change reported from the Arctic. Forest plot shows responses to climate change by 91 populations to from 40 studies. Data represent calculated absolute (left) or directional (right) effect sizes ± 95% confidence interval for each population. The size of each central data point is proportional to the precision of the estimated effect size (see footnote i). The summary effect size for each type of effect size is marked with an "S" on the x-axis (see Table 4). Grey polygons show summary effect sizes and confidence for levels of two fitted structural moderators: left, the type of data collected on the population; right, the type of response recorded by the population. See text for more explanation.

RESULTS

DATA COMPILATION

Sufficient data was available from 40 observational studies, which provided data on 91 independent populations of 49 different taxonomic groups (Figure 1). A further 66 studies reported responses but provided insufficient data, and it was decided not to seek data from authors due to time constraints. Examples of data used included: data shifts of tree margins from reconstructed age data (Jepsen *et al.* 2008), helicopter surveys of bird colony sizes on oceanic islands compared with historical records (Gilchrist & Mallory 2005), and long-term monitoring of freshwater microorganisms (Hampton *et al.* 2008). A sample of 142 data points (81 species) from 14 experimental studies was included. Most observational responses were significantly different from zero, whereas experimental data was mostly non-significant. See Figure 2 for study locations, Appendix II: Meta-analytical Database for studies used and rejected.

Figure 2: The geography of Arctic climate change research. Map shows locations of studies included in this meta-analysis. While responses have been reported from around the arctic and subarctic, there is a clear bias in study location towards certain regions, such as Alaska and Scandinavia. Multiple experimental and observational studies were carried out at or near Abisko Scientific Research Station, Tornetrask, Sweden, and Toolik Field Station, Brooks range, Alaska, but at this scale these can only be represented as a single point, the blue triangle near the corresponding label on the map. Azimuthal Projection.

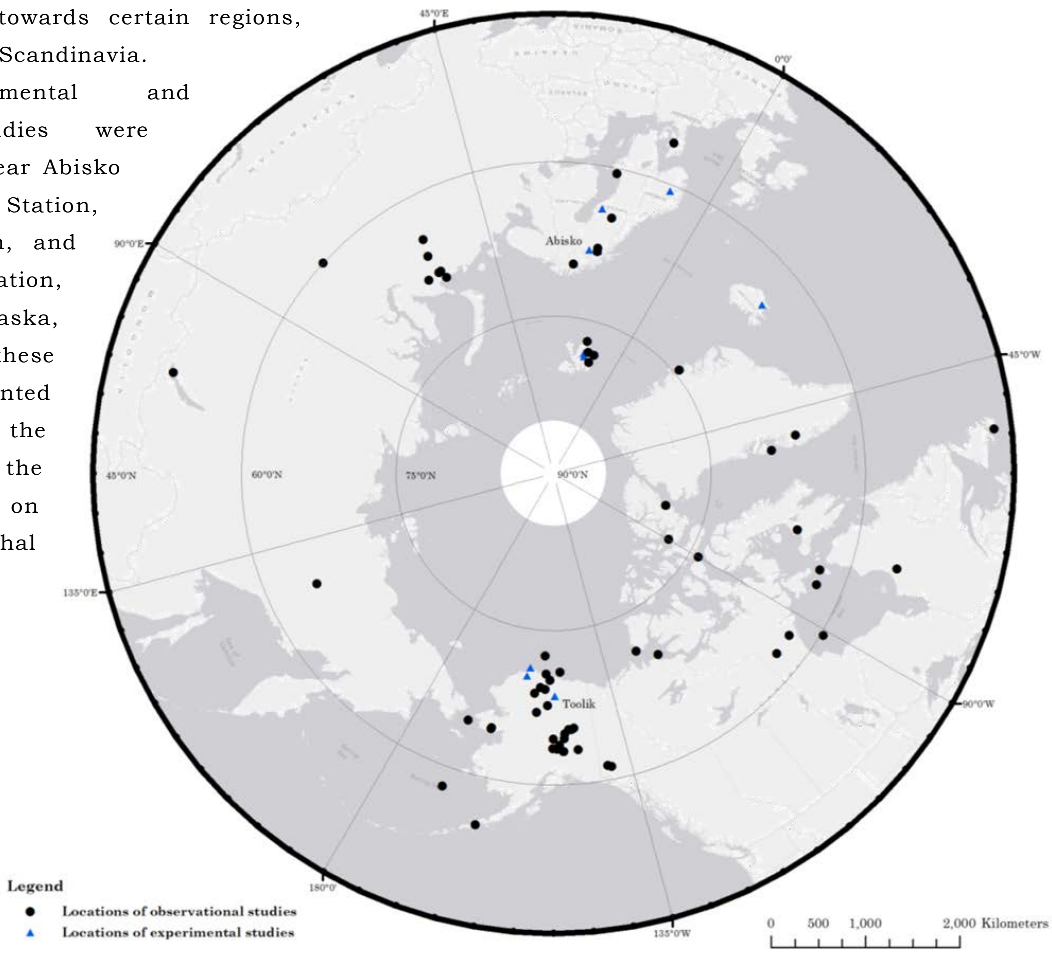


Table 4: Statistical data from fixed-effects modelling for summary effect sizes on the two overall datasets using both absolute and directional effect sizes.

Data		Summary			Heterogeneity		Fail-safe number
		effect size ±SE	z	p	Q-value	p	
Observational	Absolute	1.14±0.011	100.92	<0.0001	3577.11	<0.0001	241167
	Directional	1.06±0.011	93.89	<0.0001	4946.44	<0.0001	208729
Experimental	Absolute	0.0041±0.0041	1.0054	0.3147	203.48	0.0005	N/A
	Directional	0.0007±0.0041	0.17	0.8640	204.46	0.0004	N/A

META-ANALYSIS

SUMMARY MODELLING

The summary absolute and directional effect sizes of observational data were significantly different from zero (see Table 4), whereas the summary effect sizes of experimental data were not significantly different from zero. Both datasets, had highly significant unexplained variation, although the level of heterogeneity in the observational dataset was an order of magnitude greater. The fail-safe numbers for the observational dataset are over 200,000, suggesting that publication bias is not affecting these findings.

MODERATOR MODELLING

Models were run for all variables across both study types and with both treatments of the effect size, however for brevity only relevant results are reported here. For consistency, only analyses using the absolute effect size will be reported: no analyses had significantly greater explanatory power when fit to directional effect sizes, probably due to the small number of negative effect sizes (10/91) in the dataset and the limitations of the metafor package. Using the absolute effect size will therefore prevent negative responses from confounding analysis of the magnitude of responses.

STRUCTURAL EFFECTS

There was a significant effect of study on response magnitude across the entire dataset (experimental vs. observational, $p<0.001$, also see Figure 1 and Table 4), as expected from the summary modelling. It is likely these findings are because the experimental dataset has fewer studies, but these studies are far more comprehensive in reporting of results, especially non-significant results. The two datasets also had highly different levels of heterogeneity, thus using both datasets together in further analysis would have been inappropriate, and since more detailed analyses were carried out by Elmendorf *et al.* (2012), no further detail of experimental analyses will be reported here.

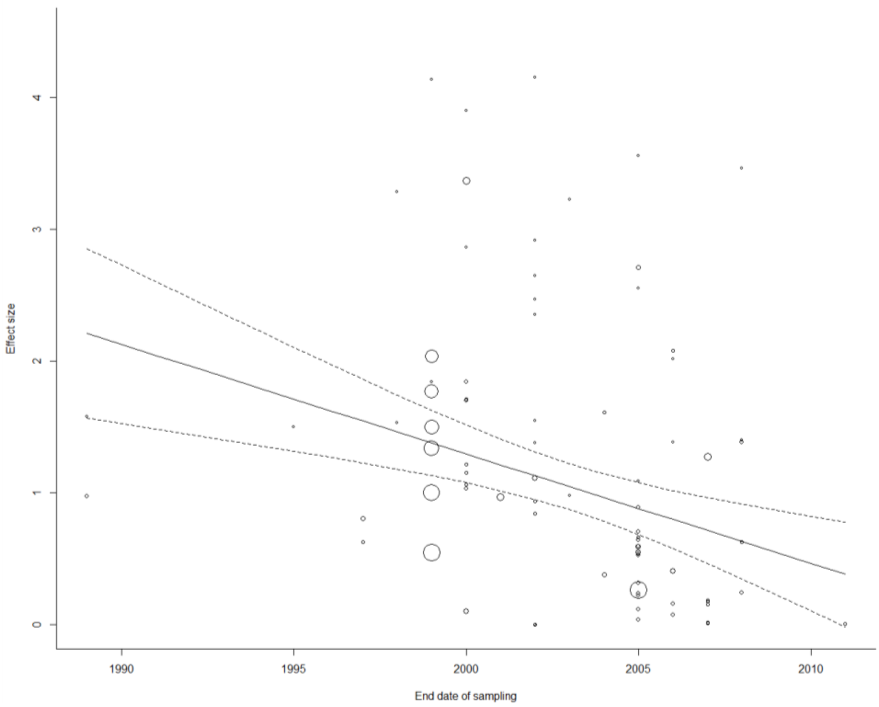


Figure 3: Variation in effect size against timeframe of study conclusion. Data represent absolute effect size for each population in the observational dataset against the year that sampling ended for the study. Size of circles is proportional to the variance of the effect size (i.e. smaller circles are more precise estimates). Linear regression (solid line) and 95% CI (dashed lines) obtained by moderator analysis (see text). One outlier included in analysis but omitted from plotting.

Within the observational dataset, there was significant between-study variation in effect size (QM=177, p<0.0001), which explained 75% of the total amount of heterogeneity found in random-effects fitting of the observational dataset alone (τ^2_{total}=0.6434, $\tau^2_{studies}$=0.1584). However, there was still significant amount of residual heterogeneity between effect sizes within studies (QE=1419, p<0.0001). Study could not be fitted as a factor in further analyses because it is not fully crossed with other categorical explanatory variables[ii(p7)], which may limit the ability to control for variation in sampling techniques or other non-ecological variation between studies. No significant effect of the type of reported response was found (QM=12.61, p=0.13), which might be assumed to encompass any broad-scale variation in sampling techniques. However, there was a significant difference between effect sizes calculated from means and all other data types (z=3.33, p=0.0009), so this was included in later analysis to control for this structural variation. There was also a significant effect on responses by the end-year of sampling (QM=13.45, p=0.0002, Figure 3) and between the types of climate change reported (time or temperature, z=3.53, 10.00, p<0.001). Fitting data type, end-year of sampling and type of climate change reported in a model explained 37% of the total heterogeneity (τ^2_m=0.4056), with significant residual heterogeneity (QE=1832, p<0.0001).

EXTRINSIC EFFECTS

There was sufficient data to fit all extrinsic effects in one model along with the significant structural effects. No significant effect of the degree of climate change recorded was found, fitted as an interaction with type of climate change to control for the differences between time and temperature data (z=0.15, p=0.67, Figure 4c&d). There was also no significant effect of latitude or longitude on the magnitude of responses (lat*long z=0.544, p=0.59; lat z=1.318, p=0.187; long z=-0.670, p=0.50, Figure 4a&b). Significant differences in responses were found between different regions and different habitat types, and these were best explained by a significant difference between the sea habitat type and all other habitat types (z=2.32, p=0.02, also see Figure 5). This term fully encompassed differences within biome or region, and no other significant landscape- or habitat-level differences were found.

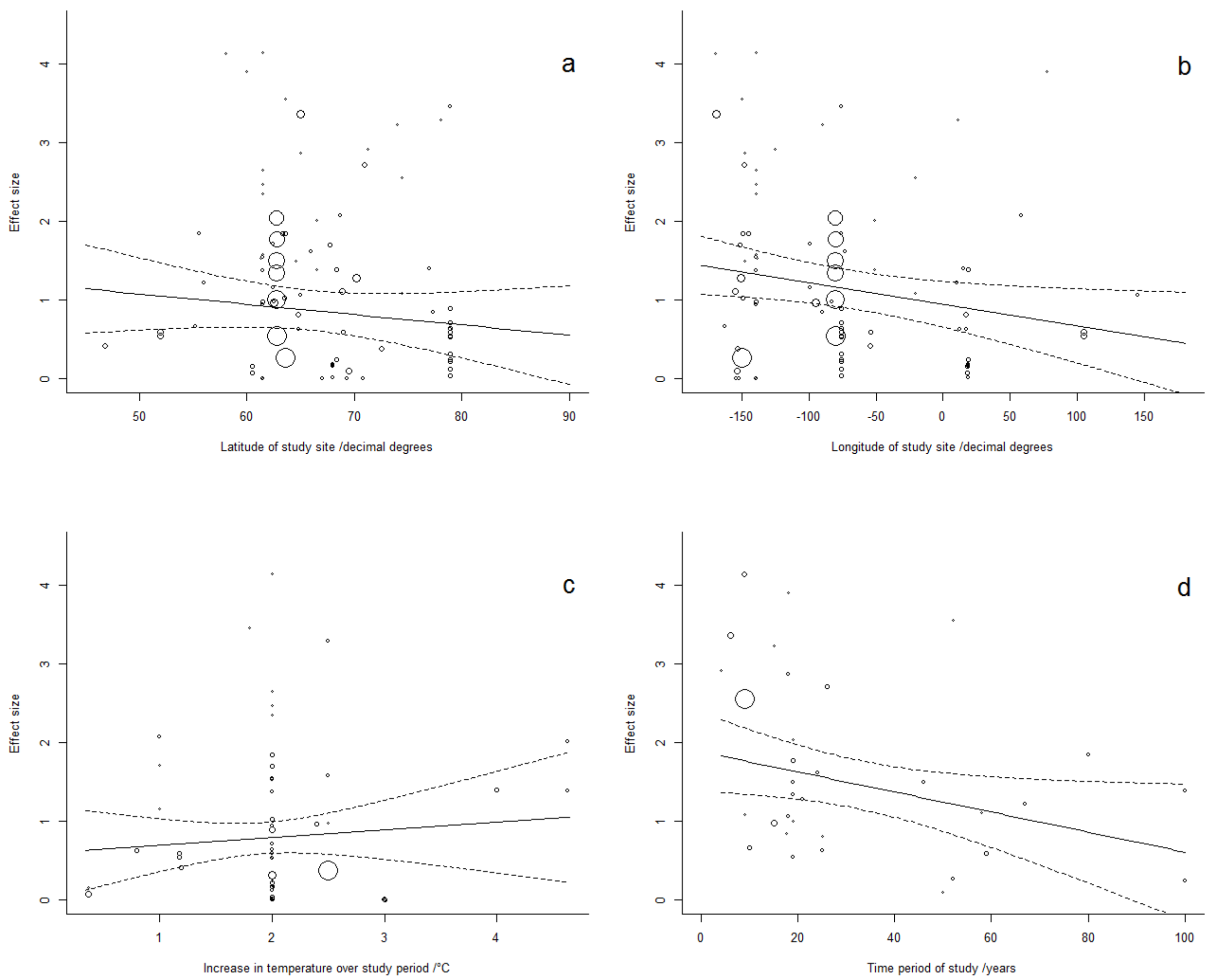


Figure 4: Variation in effect size against study characteristics. Plots illustrate **non-significant** relationships between three variables and absolute effect sizes. Size of circles is proportional to the variance of the effect size (i.e. smaller circles are more precise estimates). Linear regression (solid line) and 95% CI (dashed lines) obtained by moderator analysis (see text). a and b: latitudinal and logitudinal gradients in effect sizes. c and d: the degree of 'climatic change' over which the recorded responses occurred; data split by type of 'climatic change' recorded, temperature or time (with qualitative link to temperature). One outlier included in analysis but omitted from plotting.

INTRINSIC EFFECTS

Due to the problems with fitting nested effects in metafor[ii(p7)], it was not possible to model variation in effect size due to taxonomy or guild structure in a truly rigorous way, as this information is obviously not fully crossed. Instead, models were run for each taxonomic grade and guild level, including significant terms from the other variable categories, with the results tabulated in One outlier included in analysis but omitted from plotting..

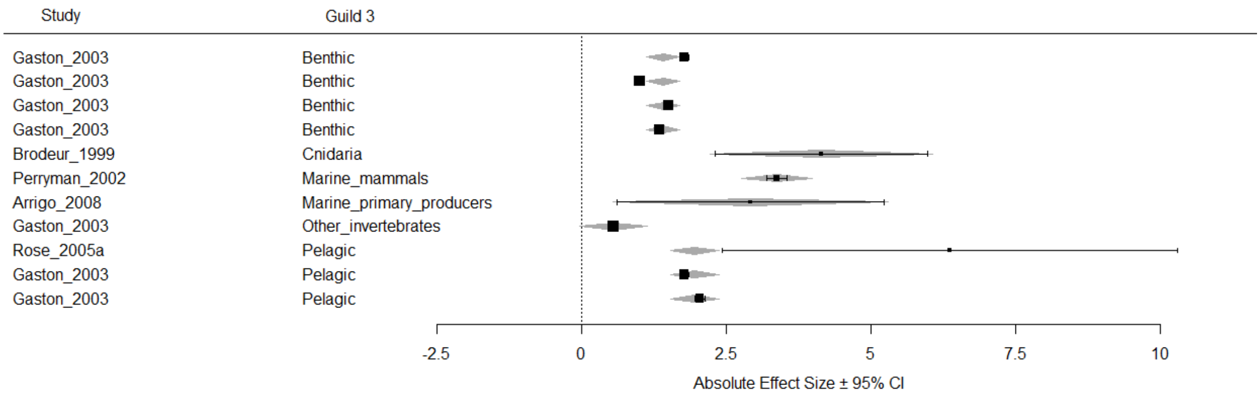
The most variation was explained at the taxonomic level of L5, broadly equating to order-level, and the narrowest guild category, which also very roughly equates to order level.

The magnitude of the estimated effect of significant factors on the overall effect sizes varied depending on the other factors fitted, and it was not possible to fit a complete model, so precise effect estimation was not possible. The signs of estimates were consistent across different models, however, and are presented in Table 6.

Term included	**Heterogeneity**		**Significant factor levels**
	% explained	τ^2	
L9≈kingdom	31%	0.4442	none
L8≈phylum	42%	0.3723	none
L7≈subphylum/class	28%	0.4629	none
L6≈class/subclass	11%	0.5718	Asterids (p=0.0241)
L5≈subclass/order	45%	0.3551	Carnivora (p=0.0795) Cetacea (p=0.0111) Ericales (p=0.0046) Pinales (p=0.0091)
L3≈family	34%	0.4235	Ericacaceae (p=0.0070) Eschrichtiidae (p=0.0094) Piceae (p=0.0172)
L2≈genus	30%	0.4503	Cassiope (p=0.0076) Eschrichtius (p=0.0144) Picea (p=0.0255)
L1≈species	37%	0.4055	C. tetragona (p=0.0058) E. robustus (p=0.0080) S. lanata (p=0.0341) P. glauca (p=0.0186)
Guild1	32%	0.4398	none
Guild2	51%	0.3163	none
Guild3 (broadest categories)	57%	0.2758	Benthic fish (p=0.0076) (Figure 5) Marine invertebrates (p=0.0012) Shrubs (p=0.0222)

Table 5: Results of fitting models for different taxonomic grades. L4 excluded as levels not meaningful when not nested. All models had significant residual heterogeneity. Levels of a term that are significantly different from the other levels of that term are noted.

Figure 5: Summary marine responses to Arctic climate change. Forest plot shows the responses of 11 marine populations to climate change. Responses are displayed as calculated absolute effect sizes ± 95% confidence interval for each population. The size of each point is proportional to the precision of the estimated effect size. Grey polygons show summary effect sizes for each level of Guild3 (Table 5)



Variable	Factor level	Sign of estimate
Study type	*Observational*	*Positive*
Data type	Means	Positive
Unit of climatic change	Years	Positive
Sampling end date		Negative
Habitat group	Sea	Positive
L6	Asterids*	Positive
L5	Carnivora	Positive
	Cetacea: Eschrichtiidae: E. robustus	Positive
	*Ericales†	Positive
	Pinales◊	Positive
L3	†Ericacaceae○	Positive
	◊Piceae•	Positive
L2	○Cassiope tetragona	Positive
	•Picea‡	Positive
	Salix▫	Positive
L1	▫S. lanata	Positive
	‡P. glauca	Positive
Guild 3	Benthic fish	Negative
	Marine invertebrates	Negative
	Shrubs	Negative

Table 6: Signs of estimates of significant effects and factor levels within effects. The estimates of omitted effects and factor levels were not significantly different from zero. Symbols in factor levels denote nesting, to highlight where significance in higher-level variables (i.e. higher taxonomic grades) may be due to significance in lower-levels. Where higher-level factors only contain one lower-level factor in the dataset, these are included together (e.g. Cetacea only contains one family, Eschrichtiidae, one genus, Eschrichtius, and one species, robustus).

DISCUSSION

SUMMARY EFFECT SIZES

These findings agree with the conclusions of global meta-analyses such as Parmesan and Yohe (2003), that species and ecosystems are clearly responding to changes in climate. However as expected, and as Elmendorf *et al.* (2012) found in their analysis of experimental results, there is a substantial degree of heterogeneity in the magnitude of these results, although there seem to be broad concordance in directionality within most types of response (Figure 1). However, the approach that was taken in this study has revealed many limitations in both data and methods, that should be considered before further ecological discussion.

LIMITATIONS

THE LITERATURE

There are considerable problems and biases in the current literature of climate change responses. The results of this study show very high inter-study variation in responses, not all of which is explained by ecological factors, suggesting a substantial effect of methodological variation. Many study areas lack standardised methodologies such as dendrochronology, which limits the ability to generalise results and confounds analyses. Unfortunately, long-term studies often have little protocol choice, as they must conform with previous work no matter how flawed or varied the methods. Similarly, the taxonomic focus of studies relies on the existence of previous datasets, perhaps the reason for the skew towards common or charismatic species such as certain plants, birds and large mammals in the literature. This focus worryingly ignores that the species most negatively affected by climate change are those with limited distributions (Thomas *et al.* 2004).

Furthermore, there are also differences in the completeness of data reported: while experimental studies frequently report the results of simulated change on every species in the studied plots, observational studies usually report only a single response, and usually only when significant. In observational studies, the majority of non-significant results were only published where the study also found significant results within their sampling protocol. That said, fail-safe analysis suggests that over 200,000 reports of non-significant population responses are required to nullify the findings, so publication bias is unlikely to affect the broader results of this study: however, these differences certainly limit the ability to quantitatively compare between experimental and observational results.

Another problem in the literature is the failure to report basic summary statistics usable in meta-analysis. Most studies carry out statistical analyses, but in many cases, particularly in higher-impact and more recent journals, these are complex, often multivariate, and do not provide simple estimates. While these analyses are of course excellent for studying complex compartmentalisation of variance, authors and editors often seem to forget the benefits of mentioning the quantity of observed changes and associated confidence.

THIS STUDY

This study has also been limited by the current state of meta-analytical techniques, as outlined above (p6). The variety of response types and data types included in this analysis generated considerable heterogeneity, and while it is possible to explain this heterogeneity in a piece-wise fashion, it cannot be precisely statistically controlled for due to the lack of nesting and fully-crossed factors in meta-analysis. While previous studies have used meta-analysis on similar (although larger) observational datasets, none found have attempted moderator analysis to explain heterogeneity in the summary effect size reported, so the methods and findings in this study could not be corroborated. The findings of this study are therefore conservative, as significance testing for ecological effects is confounded by unexplained structural heterogeneity. Thus significant findings may therefore be given some credence, although the precision of their estimated effect on responses is questionable, hence limiting the findings only to consideration of the sign of the estimate.

EXPLAINABLE HETEROGENEITY

STRUCTURAL SOURCES

As Post *et al.* (2009a) predicts, these findings display considerable response diversity. Results from the analyses of structural effects suggest that while a large degree of heterogeneity is explained by between-study variation, little is due to differences between response types. These encompass the major methodological differences between studies, and suggest that it was valid to compare across these studies. Some heterogeneity was explained by data type, and this may be because the reporting of means does not take into account fluctuations in response between the two time slices surveyed, hence authors may select the largest observed change to report, resulting in significantly larger effect sizes than in non-mean data.

Both study end date and the type of climatic change used as an explanatory variable had significant effects on the magnitude of responses. However, while end date varied by up to 22 years, and temperature has increased by an estimated 1-2°C over this time (ACIA 2004), responses decreased in magnitude over time (Figure 3), suggesting the rate of response is levelling off across populations. Alternatively, this may demonstrate a publication bias: earlier studies will have had more limited datasets, resulting in publication of only those responses of a high enough magnitude to show statistical significance. As sample sizes increased over time, researchers have more statistical power and thus can report smaller responses. The difference in effect sizes between studies that analyse response to temperature change and those that analyse response over time may be explained similarly: those that study temperature are more likely to find a larger effect size because they require a longer dataset to uncover the temperature signal with the same statistical validity. It is clearly useful that these factors were taken into account in further modelling.

EXTRINSIC SOURCES

The degree of climate change (i.e. temperature or time, Figure 4c&d) had no effect on the magnitude of response, which suggests that either this relationship is confounded by other effects or that responses occur in reaction to a threshold value of climate change rather than a simple relationship. Studies simulating climate change show that magnitude of responses do vary with degree of imposed temperature change (Aerts *et al.* 2006) suggesting that in this case the dataset is not sufficiently broad in terms of magnitude of responses or climatic change. There were also no significant broad-scale spatial trends in responses (Figure 4a&b), although the latitudinal range of the studies included was somewhat narrow. Climatic change is certainly predicted to impose varying temperature changes in different areas (ACIA 2004), but these findings may suggest either limited variation in climatic change thus far, or landscape-level buffering of its impacts. This is supported by the lack of significant variation in responses between different land habitats. Most arctic land habitat is highly limited, so it may be that rate of change in magnitude of responses are currently equivalently limited across the region, and will only differentiate on a broad spatial level when the rate of climatic change increases. It is unsurprising, therefore, that the only significant habitat-type level difference is between the land and the sea; however, as the sea is suggested to buffer climatic changes (Domingues *et al.* 2008), it is surprising that the response of sea-dwellers is significantly greater than land-dwellers (note that this category does not include species reliant on sea-ice). A possible suggestion is that marine species experience a more consistent climate trend due to the reduced fluctuation of temperature in water. Furthermore, aquatic habitats may be likely to be under greater anthropogenic pressures from fishing or pollution, which may exacerbate responses.

INTRINSIC SOURCES

Taking account of variation from structural and extrinsic sources, some taxonomic groups and guilds show significantly different responses compared with other groups/guilds in their respective grade. However, these findings may be substantially limited by the lack of nesting in models. For example, the significant difference between the responses of *Cassiope tetragona* and other species (Table 5) may well be the cause of the significance of the levels of the higher taxonomic grades encompassing *C. tetragona*; alternatively, there may be true significance between Ericales and other levels in L5, as well as further variation within the grades including *C. tetragona*. Nonetheless, the results do show that responses are idiosyncratic between the family and species level, and that communities within higher-level groupings tend not to respond similarly. Only the narrowest guild category showed any significant explanatory power. Benthic fishes and marine invertebrates (i.e. plankton) showed a significantly lower response than other guilds (Table 6), suggesting in the first case that the effects of climate change reduce with sea depth, which is to be expected. With regard to plankton, it may be that this passive, current-dispersed guild is more naturally resilient to climatic variation. Coupled with the findings with regard to the sea in general, a general conclusion may be that responses in the marine system are more clearly delineated than on land, explainable by greater homogeneity *within* the habitats of a marine system, resulting in less heterogeneity in responses.

UNEXPLAINABLE HETEROGENEITY

The models explaining the highest amounts of heterogeneity were the initial test of study-level variation (75%) and the model including all significant structural and extrinsic effects plus Guild 3 (57%), both of which had significant unexplained heterogeneity. There is thus a great deal of variation between responses, and much may be explained by differences between the methods used to study responses, the study locations and the species studied. However, there is considerable variation that is not covered by any of these explanations, and so perhaps may be put down to stochasticity, complex interactions, or response patterns that this analysis was not capable of uncovering. Furthermore, the moderators tested did not manage to explain all study-level heterogeneity, suggesting that studies are not reporting sufficient data that might be able to explain variation between responses. There could well be substantial microclimatic variation, species-level interactions, or unmeasured within-community changes, for example, that are affecting the magnitude of responses. Moderator analyses did not take account of the direction of responses due to limited data, but summary analysis found that heterogeneity was unsurprisingly even greater when taken into account. Thus the percentages stated earlier may even be an underestimate of explainable heterogeneity.

These findings have substantial implications for climate change response predictions. If it is not possible to fully explain variation in observed responses, how can researchers predict future responses with a credible degree of confidence? This has implications for conservation planning, as uncertainty is not helpful in shaping policy or attracting funding. It seems that the degree of ecological complexity is currently too great to be able to make broad predictions. However, the majority of results showed a positive trend, suggesting that in most cases, the populations of arctic and subarctic studied are 'benefitting' from climate change, in terms of increased productivity or range, for example. That said, these changes may inevitably come at a cost, for example to unstudied species that are being outcompeted or over-exploited (Forchhammer *et al.* 2008), or in the eventual invasion of the arctic by northern temperate species (e.g. Jepsen *et al.* 2008).

COMPARISONS WITH EXPERIMENTAL DATA

The findings from analysis of observational data broadly concur with the findings of Elmendorf *et al.* (2012) and this study's experimental results: that considerable levels of heterogeneity exist in species responses across both types of research. Heterogeneity is greater in observed responses by orders of magnitude, as would be expected by the greater diversity of study taxa, methodologies, responses, and uncontrolled ecological variables. Despite this, the existance of experimental heterogeneity does support the conclusions that ecological, rather than structural, response unpredictablity does occur. Elmendorf *et al.* (2012) and this study show response diversity is occuring at multiple levels, both within and between species and guilds, and across habitats.

FUTURE

Meta-analysis is a fast-moving field of statistics, and the restrictions encountered in this study will likely be resolved soon. The current main limitation in research into variation in climate change responses is the quality and completeness of the literature. Expanding the geographic scope of data collation is an option, but would result in an concomitant increase in heterogeneity and thus the amount of explanatory data. An immediate improvement over the current dataset would be to request missing data from authors; ease of future analyses could be improved by ensuring consistent and complete data presentation, even providing access to summary data online. More broadly, there is a lack of standardisation of methods across studies, with results being reported depending on data availability. It is unlikely that this will improve, hence there will continue to be limitations to the applicability of meta-analysis to such broad questions. Consistent large-scale observations may be the only way to narrow down small-scale drivers of explainable heterogeneity. There is a strong argument for creating a standardised circumpolar network of monitoring plots, similar to research in other biomes such as RAINFOR (Malhi *et al.* 2002), for more complete reporting of species responses and to allow comparisons with ITEX. Consistency is inevitably limited across biomes and study groups: one cannot measure whale migration dates using similar methods to plant biomass increases, but a marriage between both the broad meta-analysis and narrow traditional analysis routes may prove most useful in the long term.

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Citations in the EndNote style "Ecology Letters"

APPENDIX I: EXTENDED METHODS

METHODS AND CRITERIA FOR STUDY SELECTION

An initial searching stage brought together all accessible papers in peer-reviewed journals that purported to report an observed or induced response to recent or simulated climatic change in the arctic and subarctic. These studies were found through searches in the Web of Science™ (WoS) database between 22nd November 2011 and 27th January 2012 and from the references of several arctic climate change reviews and meta-analyses. The WoS search term was 'arctic AND "climate change" AND response* AND (population OR range OR distribution OR phenology OR timing OR morphology OR abundance)'. In order to decide the search terms, several pilot searches seeking known studies were run using more or less stringent operators/terms to evaluate the most effective trade-off between result comprehensiveness and number of irrelevant studies. Diversity in paper naming practices and keyword usage necessitated a broad search term. The number of returned studies on the final day of searching was 799. Titles and abstracts were inspected within the WoS results for relevance to this study, and candidates were fully examined against a set of criteria for inclusion in the meta-analysis.

1. Responses to climate change must be reported as a result of observation or experimentation. Predictions or assumed responses (e.g. modelling, physiological study) were not included, nor were the findings of reviews/meta-analyses.
2. Responses must be measured on a consistent scale within the study, reported using acceptable statistics for the calculation of effect sizes, and be in a category that allows generalisation between studies (see Table 1, Response types).
3. Papers reporting observational responses must:
    - Utilise data collected on substantially the same population(s), using the same or substantially similar methods. at two time periods not less than three years apart
    - Over the same time period, report a corresponding change in temperature or related variable (e.g. sea-ice breakup).
    - Reasonably demonstrate the observed response was not confounded by other factors.
4. Papers reporting experimental responses must:
    - Utilise consistent methods for imposing simulated climate change, and provide data on controls.
    - Report data after at least two seasons of imposed climatic change.
5. Responses must be attributed to changes in temperature or, where no direct relationship is drawn, over a time period where temperature has also been observed to have significantly changed. While there are other possible environmental changes that could elicit ecological

responses, the vast majority of observational studies only attribute the response to changes in temperature, hence this criterion was selected in order that data be comparable.

6. The study must described the study area as arctic or subarctic, a minimum latitude was not used because this does not accurately describe the distribution of these habitat types.
7. The population or individuals studied must inhabit the subarctic or arctic regions for at least a substantial portion of every year (e.g. breeding season), and reported responses must be explained by climatic changes occurring within the arctic or subarctic region. Some studies related arctic climatic changes to responses of migratory populations (arctic tern, grey whale) surveyed elsewhere (e.g. Perryman *et al.* 2002)
8. There must be no overlapping of datasets: where separate studies analyse the same response data collected on the same populations, the study with the greater statistical power was used - usually the more recent paper.
9. Sufficient data must be reported in order to calculate the relevant effect size for the observed response type.

The majority of papers failing the criteria did so because their title or abstracts presented their findings in such a light as to suggest that the paper reported a response to climate change, whereas on inspection of the methods and findings this was found not to be the case. For example, many papers presented predictive modelling as responses, analysed physiological or ecological characteristics of a species and suggested a likely response, or studied distribution patterns over climatic gradients.

APPENDIX II: META-ANALYTICAL DATABASE

OBSERVATIONAL STUDIES FULFILLING CRITERIA (40)

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