Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects

Running head: Mechanisms of climate change

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Abstract

Shifts in species' distribution and abundance in response to climate change have been well documented, but the underpinning processes are still poorly understood. We present the results of a systematic literature review and meta-analysis investigating the frequency and importance of different mechanisms by which climate has impacted natural populations. Most studies were from temperate latitudes of North America and Europe; almost half investigated bird populations. We found significantly greater support for indirect, biotic mechanisms than direct, abiotic mechanisms as mediators of the impact of climate on populations. In addition, biotic effects tended to have greater support than abiotic factors in studies of species from higher trophic levels. For primary consumers, the impact of climate was equally mediated by biotic and abiotic mechanisms, while for higher-level consumers the mechanisms were most frequently biotic, such as predation or food availability. Biotic mechanisms were more frequently supported in studies that reported a directional trend in climate than in studies with no such climatic change, although sample sizes for this comparison were small. We call for more mechanistic studies of climate change impacts on populations, particularly in tropical systems.

Introduction

Climate is often regarded as the ultimate factor determining species' distributions, although disentangling climatic influences from other factors can be difficult (Gaston, 2003; Huntley *et al.* 2007). Climate may limit species' distributions directly (Iversen, 1944; Root, 1988; Gross & Price, 2000), but in other cases the link to climate may be mediated by biotic interactions (Pienkowski, 1984; Ferrer *et al.*, 1991), and there remains considerable debate about how species' range boundaries are determined (Gaston, 2003). Climate change has greatly increased the significance of this debate. The global climate has warmed at an increasing rate over the past century (IPCC, 2007), leading to widely reported changes in distribution and abundance of species (Parmesan & Yohe, 2003; Hickling *et al*., 2006; Chen *et al.*, 2011), as would be expected if climate was limiting. Numerous studies have attempted to predict the impacts of climate change on natural populations using spatial relationships, which model species' distributions as a function of climate. Such climate change projections can then be used to estimate the potential future range of species and their probability of extinction (Thomas *et al.*, 2004; Huntley *et al.*, 2007; Hole *et al.*, 2009). Due to their correlative nature, these approaches have been criticised for being vulnerable to Type I error (e.g. Beale *et al.*, 2008). Therefore, more process-based models (e.g. Peery *et al.*, 2012) have recently been developed to improve projections of biodiversity responses to climate change (Chevin *et al.*, 2010; McMahon *et al.*, 2011) and inform adaptive conservation responses (Dawson *et al.*, 2011; Pearce-Higgins *et al.*, 2011, Hole *et al*., 2011). However, these models require knowledge about the underlying ecological mechanisms by which climate affects populations (Geyer *et al.*, 2011) and this knowledge is currently limited.

Cahill *et al.* (2013) recently reviewed the mechanisms by which climate change affects extinction risk, but found just seven studies that identified proximate causes of local extinction and eleven that examined causes of population change due to climate change. Their conclusion, based on this limited sample, was that the principal climate change related threats to populations may come from altered species interactions, rather than direct effects of temperature or precipitation. Additional insights into the mechanisms by which climate affects populations could be gained from a synthesis of the many published studies which have examined changes in population growth rates and demographic parameters in response to climatic variation. Negative effects can provide an early indication of range contractions and population declines, but positive effects may also be important, signalling potential colonisation events and range expansions. Improving our mechanistic understanding will enhance our ability to make projections of the ways that climate change will impact not just populations, but also the structure and function of ecological communities.

In this study, we use the results of a systematic review and meta-analysis of literature to investigate the mechanisms by which variation in climatic variables may drive population increases and declines. Proximate mechanisms were defined as the direct processes by which climate affects the physiology, behaviour or environment of an organism, and hence impacts survival or productivity. In addition to describing these mechanisms, we examine whether they vary spatially or between different types of species, in order to improve our understanding of species' vulnerability to climate change and inform appropriate conservation responses. Specifically we address the following four questions:

1) What is the geographical and taxonomic coverage of studies that have tested proximate mechanisms linking climate variables to population change, and do these studies exhibit biases compared to studies that do not identify mechanisms?
2) What are the most frequently supported proximate mechanisms underpinning the effects of climate on natural populations?

3) Does the importance of different proximate mechanisms vary with latitude or ecosystem?
4) Does the importance of different proximate mechanisms vary with characteristics of the species (taxonomic grouping, trophic level and endotherms versus ectotherms)?

Our review is based on studies of global terrestrial and freshwater biodiversity that reported population responses to changes in climatic variables over a period of at least 20 years. Many of these document changes in response to natural year-to-year fluctuations in the weather, rather than explicitly examining the consequences of long-term climate change. The extent to which information from these studies can be applied to an assessment of the impacts of climate change is uncertain. However, a significant subset of studies did report the trend in climate over the study period, enabling us to examine whether study systems reporting climate change were affected by the same mechanisms as those where no directional climate trend was reported.

Materials and methods

The systematic review was conducted through a literature search using ISI Web of Knowledge on 14/11/11. Key words were selected to identify demographic studies *(Population*, Demograph*, Reproduct*, Decline*, Abundance , Breeding, Survival, Mortality, Fecundity, Density, Productivity*) of climate change impacts (*Climat*, Global warming, Sea-level rise, Elevated CO2, Elevated carbon dioxide, Global environmental change*) that clearly related changes to specific environmental drivers (*Temperature*, Fire*, Glaci*, Snow pack, O2, Oxygen, Flood*, Drought*, Ground-water levels, Precipitation, Thermal stratification, Sea-level rise, Cloud cover, Humidity, CO2, Carbon dioxide, UV, Ultra violet, Water current, Salinity, Nutrient, Erosi*, Wind*, Rainfall, Storm*, Hurricane, Cyclone, Typhoon*). This generated 30,880 hits that were filtered by title and abstract and subsequently by content to produce a list of studies that correlated annual variation in demographic metrics with climate variables over at least 20 years (a period considered sufficient to detect effects of climatic variation above other processes affecting abundance). Only studies of terrestrial and freshwater taxa were retained, as marine organisms are expected to respond to different climatic variables (Burrows *et al*., 2011; Sunday *et al.*, 2012). The initial screening of titles and abstracts was carried out by three individuals (DWB, JAC and ECW), and Kappa scores were calculated across a subset of 400 papers to check for consistency between reviewers. Discussion between reviewers resulted in reasonable consistency (Kappa score >0.6) for all pairs of reviewers. Once the contents filtering stage was reached, each study was scrutinised by at least two people, and any discrepancies were discussed until a consensus decision was reached. The screening retrieved a final set of 146 studies investigating the effects of climate on demography, covering 1,543 separate analyses of population time-series. The majority of these examined variation in temperature (53 studies) or precipitation (69 studies), while 22 reported variables that were combinations of temperature and precipitation effects. A further 37 studies included a variable describing changes in large-scale circulation patterns (NAO or ENSO), six contained variables that related to storm frequency or wind strength, while one study tested variation in fire frequency.

Publication bias

Of the 146 studies identified in the literature search, 87 tested one or more proximate mechanisms that could underpin the relationship between climate and demography (abundance, productivity or survival), totalling 273 separate tests. Studies were only considered to have tested a mechanism if it was specified in the introductory or methods sections of a paper, rather than used as a *post hoc* explanation for observed correlations.

We first tested for publication bias in the type of study that examined mechanisms compared to those that did not. This was achieved by modelling the proportion of population time-series analysed that tested for a proximate mechanism as a function of several possible bias variables. Models were constructed using a generalised linear mixed model (GLMM) with a binomial error distribution and logit link function. Study identity was included as a random effect to account for the non-independence of separate time-series or climate variables analysed within the same study. Explanatory variables tested in the model were study duration (in years), latitude (degrees from the equator), taxonomic group (split into birds, mammals, fish, invertebrates and plants; amphibians were excluded as only four time series were found) and ecosystem (two-level factor separating freshwater from terrestrial). All analysis was conducted using SAS software version 9.2 (SAS Institute, 2008).

Proximate mechanism support

The relative importance of different mechanisms was assessed by modelling whether or not the *a priori* expectation was supported for each population time series. Mechanisms were split into categories and subcategories based on previous studies (Geyer *et al.*, 2011, Cahill *et al.*, 2013), and were also separated into biotic (indirect) and abiotic (direct) factors (Table 1). Biotic mechanisms describe processes where the effect of climate on the focal species is mediated via effects on another species, such as changes in food resources or predator populations, while mechanisms were classified as abiotic if the climate variable affects the organism directly, such as heat-stress leading to a reduction in survival. We followed the analytical framework outlined above, using a GLMM with binomial error distribution and logit link function. The response variable was the 'support index', calculated as the proportion of tests of a mechanism that were supported in a study. If only one test was carried out then the index had a value of 0 or 1, but in many cases there were multiple tests of a mechanism (using several climate variables or a range of demographic responses to examine a single mechanism), some of which may have been supported, while others were not; the support index allowed us to account for this in our analysis. The explanatory variable was the mechanism category.

Mechanisms were classified according to the level of evidence provided to support their role in effecting the impacts of climate. They were categorised as: (i) unsupported by published studies (19 cases); (ii) supported by published studies from a different, but ecologically or taxonomically similar, species (103 cases); (iii) supported by published studies on the same species from a different population (51 cases); (iv) supported by published studies from the same population (57 cases); (v) demonstrated within the focal study (43 cases), which in many cases were independent measures of the mechanism of interest, such as variation in prey or predator abundance, that were reported in the same paper. Mechanisms backed by higher levels of evidence (i.e. from the same species) were more frequently supported than those based on no published evidence or evidence from a different species ($F_{1,182} = 5.4$, $P = 0.02$). In order to reduce this bias we based our main analysis of mechanism importance on those mechanisms supported by evidence from the same species only, which was either presented in the same paper or cited in another study of the same species (categories (iii) – (v) above). This gave us a dataset of 151 tests of mechanisms across 64 studies for the main analysis (study details shown in Appendix S1). However, results of analyses including data from studies based on all levels of evidence were qualitatively similar, and are presented in Appendix (S2).

Variation in proximate mechanism support

Following the same analytical approach of using a GLMM to model the support index, we tested whether mechanism support differed with respect to variables relating to the study system (latitude and ecosystem) and ecological traits of the study species (taxonomic group, thermal strategy (endotherms versus ectotherms) and trophic level (primary producers, primary consumers and secondary or higher consumers)). This was achieved by testing the significance of the interaction term between each variable and mechanism category. For this, mechanism category was simplified into biotic versus abiotic factors, in order to provide sufficient within-category variation for the analysis.

The same climate variable may affect different populations via different mechanisms, depending on their demographic response to that variable. For example, a negative population change in response to warming may be underpinned by a different mechanism to a positive response. For studies where a significant relationship between demography and either temperature or precipitation was detected, we tested whether the direction of this relationship (modelled as a logistic regression where 1 was positive and 0 negative) varied between mechanism-types.

Finally, we tested whether mechanism importance varied between studies which reported a directional trend in the climate variable over the study period, and those which did not. This was achieved using a subset of studies in which such information was presented, by interacting mechanism categorisation (biotic versus abiotic) with a two-level factor describing climatic trend (present or absent).

Results

Publication bias

The 146 studies of the effects of climate on populations that were identified by the systematic review included 352 separate analyses of population time series, of which 162 were of bird populations, 74 mammals, 52 invertebrates, 21 fish, 4 amphibians and 39 plants (35 of which were trees). The majority (301) of species were terrestrial, with just 51 freshwater species examined. Of the animals, 141 were primary consumers and 172 secondary or higher-level consumers. The vast majority of studies were carried out at temperate latitudes (35˚ - 70˚) of North America and Europe (Fig. 1).

Over half of the studies identified in the literature search (87 of 146) tested at least one *a priori* proximate mechanism linking the effects of climate with demography. There was no significant difference in latitude ($\chi^2_1 = 2.2$, $P = 0.14$), ecosystem (terrestrial versus freshwater: ($\chi^2_1 = 2.3$, $P = 0.13$), trophic level ($\chi^2_2 = 0.28$, $P = 0.87$) or study duration ($\chi^2_1 = 0.51$, $P = 0.47$) between studies that did and did not test a proximate mechanism. However, there was a statistically significant difference in the likelihood of testing a proximate mechanism between taxa ($F_{4,207} = 2.9$, $P = 0.02$), which was largely driven by significant contrasts between mammals (where 73% of studies tested a mechanism) and fish (18% studies tested a mechanism, $F_{1,270} = 9.4$, $P = 0.002$) and between mammals and invertebrates (47% tested, $F_{1,176} = 4.82$, $P = 0.03$).

Proximate mechanism support

The level of support varied between different mechanism types ($F_{5,77} = 2.5$, $P = 0.04$; Fig. 2), driven by significant contrasts between predation and all other mechanism types ($P < 0.03$ for all contrasts with predation). Overall, biotic mechanisms were significantly more frequently supported by the evidence than abiotic factors ($F_{1,86}$ =6.1, P =0.02).

Variation in proximate mechanism support

The relative importance of biotic versus abiotic mechanisms did not differ with latitude ($F_{1,84}$ =0.6, P =0.44), species' thermal strategy ($F_{1,84}$ <0.01, P =0.92), taxonomic group ($F_{4,80}$ =0.73, P =0.57) or ecosystem ($F_{1,85}$ =0.14, P =0.71), but did vary with respect to trophic-level (interaction between trophic level and mechanism-type, $F_{1,83}$ =5.96, P =0.02, Fig. 3). Investigations of the effect of biotic factors on plants were rare (only two out of twenty tests amongst producers were of biotic mechanisms, which were therefore excluded from this comparison) while only 11% of tests of abiotic mechanisms were supported among plants. Primary consumers appeared equally affected by both biotic and abiotic mechanisms, while populations of higher consumers were most strongly affected by biotic mechanisms (Fig. 3).

The relative importance of biotic and abiotic mechanisms varied with the direction of the relationship between precipitation and population metrics ($F_{1,31}$ =7.1, P =0.01). Abiotic mechanisms were more likely to be underpinned by negative effects of precipitation, while biotic mechanisms were more likely to drive positive population responses to precipitation. There was no equivalent contrast in the relative importance of different mechanism types between studies of the positive and negative effects of temperature on populations ($F_{1,27}$ =2.1, P =0.16).

Results from studies documenting climate change

Of the 64 studies which tested a mechanism mediating the effect of climate variables on demography that was supported by evidence from the same population or species, fewer than half (27) reported whether there was a climatic trend over the study period. Among these 27 studies, there were 64 tests of the effect of climate on demography, of which 39 (61%) reported a directional change in the climate variable tested. Among studies that reported no trend in climate variables through time only 9% of tests on population time-series supported a mechanism compared to 44% in studies which did report a directional change in climate, although this difference was non-significant ($F_{1, 36} = 2.46$, $P = 0.13$). The previously identified contrast in the relative importance of biotic and abiotic mechanisms was detected only in studies where a significant change in climate had been observed ($F_{1. 34}= 7.47$, $P = 0.01$; Fig. 4).

Studies that reported climate trends were much more likely to be of higher consumers than primary consumers. While 46% of studies of higher consumers showed a climatic trend, only 4% of studies of primary consumers did so; climate trends were not reported in 37 % and 80% of studies respectively. Therefore, it is possible that the previously identified contrast in the importance of biotic versus abiotic mechanisms between trophic levels may be partially confounded by the effects of recent climatic trends; unfortunately there were insufficient data to thoroughly analyse this possibility.

Discussion

Proximate mechanism support

Our principal finding is that biotic mechanisms, associated with altered species interactions, appear to be more important drivers of the relationship between populations and climate than abiotic mechanisms describing direct effects of climate. This result provides a novel insight, as it is based on a large number of long-term studies of impacts of climate on populations, including both positive (indicative of population increases and colonisation of new areas) and negative effects (potentially indicative of extinction risk). Predation received twice the level of support achieved by other mechanisms, although this finding was based on the results of 22 tests spread over only five different studies. When the results from all studies that identified a mechanism were considered, rather than only those where the mechanism was supported by studies on the same species, then the contrast between predation and other important mechanisms, such as changes in food availability and phenological mismatch, was less clear (Appendix S2). It is the combined support for these three mechanisms (predation, food availability and phenological mismatch) that led to the significantly greater level of support for biotic compared to abiotic mechanisms.

The importance of changing species interactions was also recognised in a recent analysis of 18 studies of climate-related local extinctions, population declines and oscillations (Cahill *et al.*, 2013). Taken together, these results emphasise the need to understand the impacts of climate on interactions within ecological communities in order to fully assess the likely responses of populations to climate change. Many recent studies of species' vulnerability to climate change have focussed on climatic tolerances alone (Deutsch *et al.*, 2008; Bonebrake & Mastrandrea, 2010; Sorte *et al.*, 2011; Sunday *et al.*, 2012; Araújo *et al.*, 2013), which our results suggest are therefore likely to be incomplete. There is an urgent need for more mechanism-based assessments of the impacts of climate change on species, populations and communities. While some such studies have recently been published (Both *et al.*, 2006; Pearce-Higgins *et al.*, 2010; van de Pol *et al.*, 2010; Harley, 2011; Martin & Maron, 2012), a step-change in their frequency is required to begin to develop the level of mechanistic understanding required for realistic process-based models of climate change impacts (Chevin *et al.*, 2010; Dawson *et al.*, 2011).

Our review also revealed that while some ecological mechanisms have been examined frequently others have received scant attention, with mechanisms of direct interactions between trophic levels (predators and prey), phenological change and direct temperature and water stresses most often studied (Table 1). Given the role that inter-specific competition plays at species' range margins (Ahola *et al.*, 2007; Bridle & Vines, 2007), the absence of studies investigating competition-related mechanisms was a surprising omission, although it may be partially explained by the complexities of attributing population changes to competition.

Variation in proximate mechanism support

Biotic mechanisms were more likely to underpin studies where precipitation positively affected populations, while abiotic mechanisms were more frequent in cases where precipitation had a negative effect. Thus, the negative effects of low rainfall are most likely to impact a species via other interacting populations, such as food resources or predators (e.g. Chase *et al*., 2005), rather than by direct water stress. Conversely, populations that decline in response to high levels of precipitation tend to do so because of direct detrimental effects of flooding (e.g. Ratcliffe *et al.*, 2005) or positive effects of dry weather, such as triggering masting in beech trees (Piovasen *et al*., 2001).

We extended our comparison of biotic and abiotic mechanisms to demonstrate that the importance of different proximate mechanisms varied with trophic level. Specifically, we found that populations of primary consumers tended to be more sensitive to direct impacts of climate than higher consumers. The latter were more frequently affected by biotic interactions, with studies of Arctic foxes *Vulpes lagopus* (Hersteinsson *et al.*, 2009), badgers *Meles meles* (MacDonald *et al.*, 2010) and golden plovers *Pluvialis apricaria* (Pearce-Higgins *et al.*, 2010) all highlighting impacts of reduced prey abundance. This emphasises the need to improve our understanding of the potential for climate change to disrupt existing ecological interactions, which could be achieved by more studies that jointly monitor populations of species at different trophic levels within an ecosystem.

We found only one study showing plant populations were limited by biotic interactions (Martin, 2007), while only 11% of tests of abiotic mechanisms in plants were at least partially supported by the evidence. This shortage of studies investigating biotic processes makes it difficult to know whether the low level of support for abiotic mechanisms is due to a relative insensitivity of plants to climate change (or our inability to detect their responses), or whether abiotic interactions are less important in this taxon. Our focus on investigations of inter-annual fluctuations in demographic variables as a function of temporal variation in climate variables may have limited the number of plant studies included. We did not consider other types of study (e.g. comparisons of change across space in relation to varying climatic trends, or studies of range change or community change) that may be better able to identify certain mechanisms, such as gradual climate-induced habitat change. Many studies of plants are likely to be of these types (e.g. Foden *et al*., 2007; Virtanen *et al.*, 2010) and a review of such studies may provide additional insight into the mechanisms underpinning responses to climate change in a different suite of species.

Publication bias

There are clear limitations to our understanding of the way climate change is likely to impact natural populations, even in well-studied populations and systems. In the tropics, we know little of the potential impacts of climate change on populations, supporting other research demonstrating that tropical species are less-well studied and monitored (Amano & Sutherland, 2013). This is particularly worrying given that the majority of species, and most threatened species of global conservation concern, are concentrated at such latitudes (IUCN, 2012). The significantly lower frequency of mechanism testing for freshwater fish and invertebrates compared to mammals reveals the need for more published analyses on such taxa. This is particularly important given our finding that the impacts of climate are often transmitted between trophic levels.

Despite the biases present in the taxa and latitudes of published study systems, we have assumed no bias in the frequency with which evidence relating to the different mechanisms has been published. It is possible that some mechanisms are only investigated once a researcher is reasonably confident of their importance (for example, some of the more complex indirect mechanisms), whereas it is reasonably straightforward to test for direct mechanisms even in poorly understood systems; it is plausible that this could have led to the greater support for biotic mechanisms. It is also conceivable that biotic mechanisms could be viewed as more ‘interesting’ and hence publishable, by authors, reviewers and editors. Our observation that biotic mechanisms were more frequently supported in studies which also reported significant climatic trends may conceivably be partly due to such a publication bias.

With our current dataset we are unable to investigate these possibilities; however we found little evidence of publication bias where we were able to test for it, in relation to the proportion of studies which tested specific mechanisms.

Effects of climate change

The greater importance of biotic mechanisms relative to abiotic ones appeared more marked in studies that documented an impact of climate change than those that reported no trend in climatic variables, although this comparison was based on a relatively small sample of studies (27 studies of mechanisms supported by evidence from the same species, or 35 studies irrespective of mechanism support, presented in Appendix S2). Climate change may therefore already be having a disruptive effect on interactions between species relative to the effects of normal fluctuations in the weather.

Regardless of this comparison, our results highlighting the general importance of biotic interactions imply there is an urgent need to understand species interactions within ecological communities in order to predict the impacts of climate change (Harrington *et al.*, 1999; Parmesan, 2006; Mustin *et al.*, 2007; Devictor *et al.*, 2012). For many systems, particularly those outside Europe and North America, this will require relatively basic ecological studies on species interactions. Long-term monitoring is required to quantify the importance of different mechanisms in driving population change (Morrissette *et al.*, 2010), while experimentation may also be used to test the importance of potential proximate mechanisms (Martin & Maron, 2012). Ultimately, this information can be used to identify potential adaptation responses to climate change (Carroll *et al.*, 2011; Pearce-Higgins, 2011). However, given limited conservation resources (Scott *et al.*, 2010; McCarthy *et al.*, 2012) it is not feasible to adopt this approach for more than a small number of priority species.

Therefore, a more realistic aspiration may be to better understand the general mechanisms through which climate determines species’ abundance and distributions and by which climate change may affect population trends, in order to improve our ability to identify generic options for effective climate change adaptation, as well as highlighting where we may find exceptions to these generalisations.

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Supporting Information Legend

Appendix S1: Details of studies used in analysis

Appendix S2: Results of analysis using full data set, including papers where evidence for mechanism was absent or based on a species other than the focal species.

Tables

Table 1. Types of proximate mechanisms, their frequency in the literature, and their classification into biotic / abiotic factors.

Mechanism category	**Description**	**Subcategories**	**N**	**Biotic / abiotic**
Temperature stress	Direct impacts of temperature	Heat stress Cold-related mortality Energetic costs	26	Abiotic
Water stress	Direct impacts of too much or too little water	Desiccation / drought stress Consequences of flooding	36	Abiotic
Development rate	Direct impact on organism’s growth or development rate		8	Abiotic
Habitat	Changes in habitat extent		5	Abiotic
Phenology	Changes in phenology	Loss of interactions due to phenological mismatch Change in breeding phenology Change in migration phenology Change in breeding season length	30	Biotic Abiotic Abiotic Abiotic
Resources	Changes in resource availability	Change in food availability Change in foraging efficiency	17	Biotic Abiotic
Predation	Changes in predation interactions	Change in predator populations Change in predation risk	47	Biotic
Pathogens	Changes in pathogen populations		4	Biotic
Anthropogenic mortality	Changes in human-related mortality	Climate impacts frequency of traffic-related mortality	1	Biotic

Figure legends

Figure 1. Location of studies of at least 20 years duration relating population time-series to climate. Black dots indicate studies where proximate mechanisms were tested (N =87) and white dots those where no mechanism accounting for the relationship between climate and demography were tested (N =59).

Figure 2. Mean support index ± se (proportion of population time series for which a mechanism is supported) for each mechanism category, derived from data on mechanisms supported by evidence from the same species. Biotic mechanisms are in black, abiotic in white and mixed categories in grey. Labels on each column show the number of tests carried out (top number) and the number of studies from which the tests were drawn (bottom number). Categories labelled with the same letter do not differ significantly ($P > 0.05$); pairs of categories with non-matching letters therefore differ significantly ($P < 0.05$).

Figure 3. Mean support index ± se (proportion of population time series for which a mechanism is supported), for abiotic (white) and biotic (black) mechanisms across different trophic levels. Only data on mechanisms supported by evidence from the same species are presented. Labels on each column show the number of tests carried out (top number) and the number of studies from which the tests were drawn (bottom number). Categories labelled with the same letter do not differ significantly ($P > 0.05$); pairs of categories with non-matching letters therefore differ significantly ($P < 0.05$).

Figure 4. Mean support index ± se (proportion of population time series for which a mechanism is supported) for abiotic and biotic mechanisms between studies that document a climatic trend (black) and those that do not (white). Only data on mechanisms supported by evidence from the same species are presented. Labels on each column show the number of tests carried out (top number) and the number of studies from which the tests were drawn (bottom number). Some studies are represented in more than one column. Categories labelled with the same letter do not differ significantly ($P > 0.05$); pairs of categories with non-matching letters therefore differ significantly ($P < 0.05$).

Figure 1

Figure 2

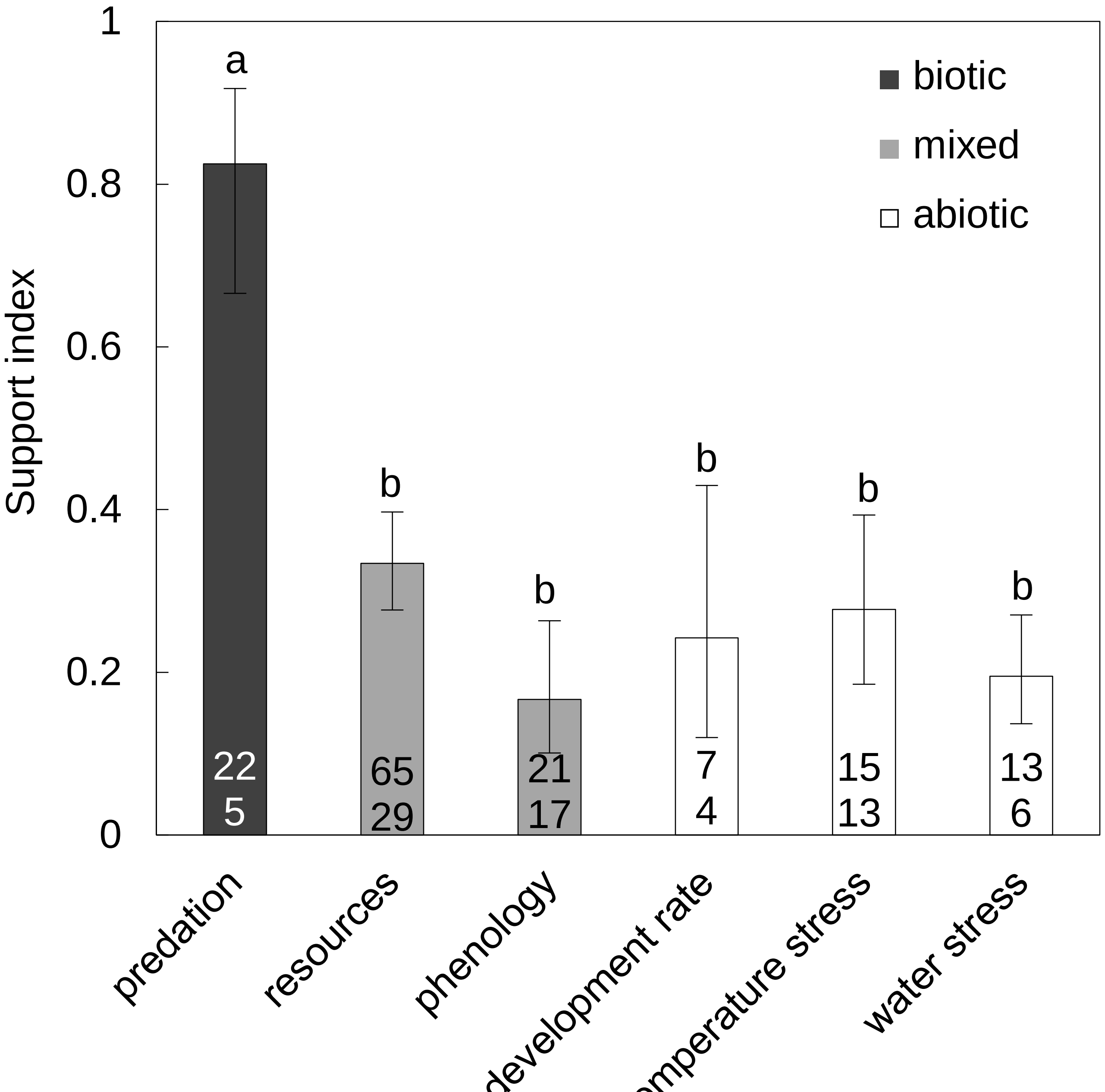

Support index
1
0.8
0.6
0.4
0.2
0
■ biotic
■ mixed
□ abiotic
a
b
b
b
b
b
22
5
65
29
21
17
7
4
15
13
13
6
predation
resources
phenology
development rate
temperature stress
water stress

Figure 3

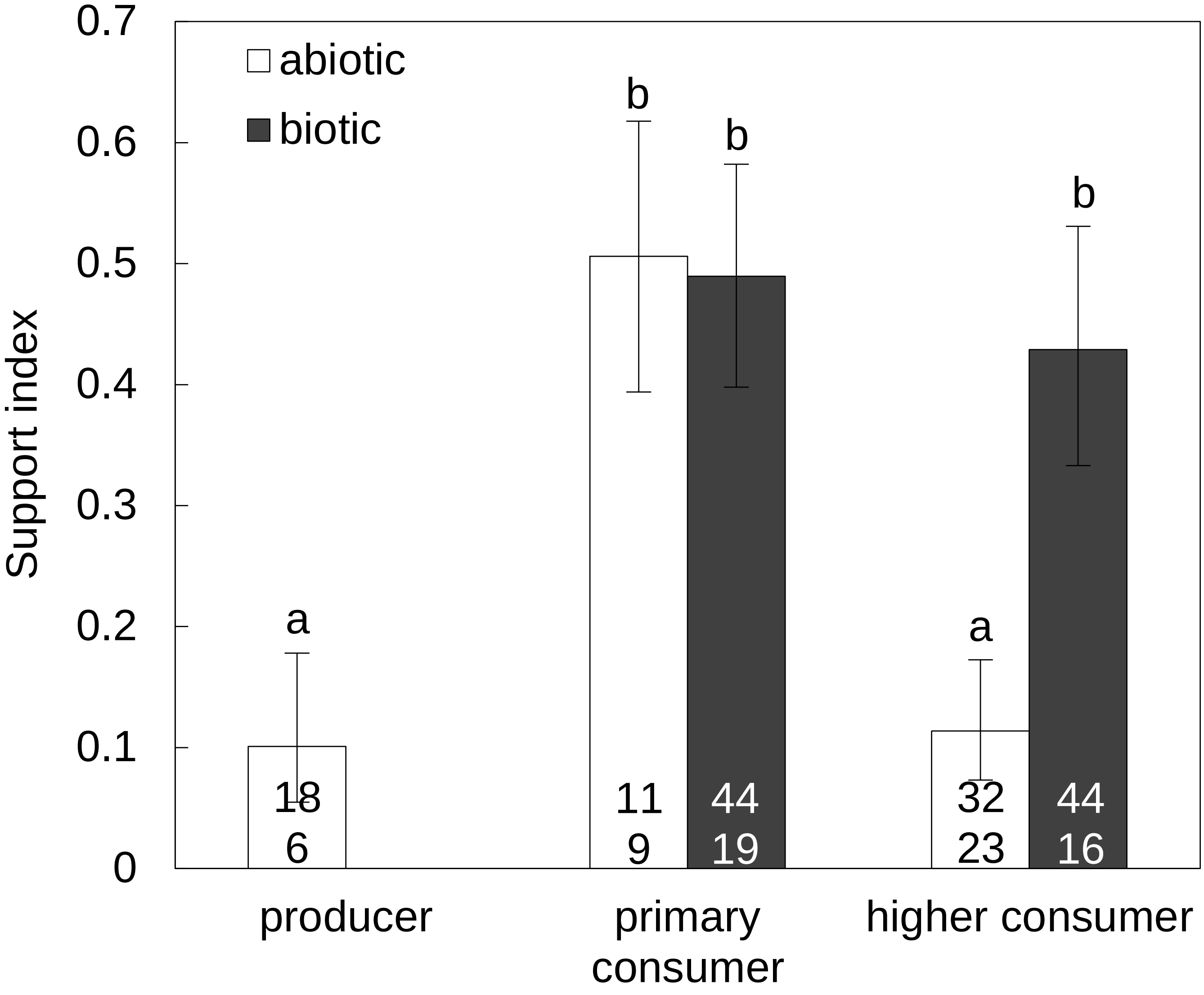
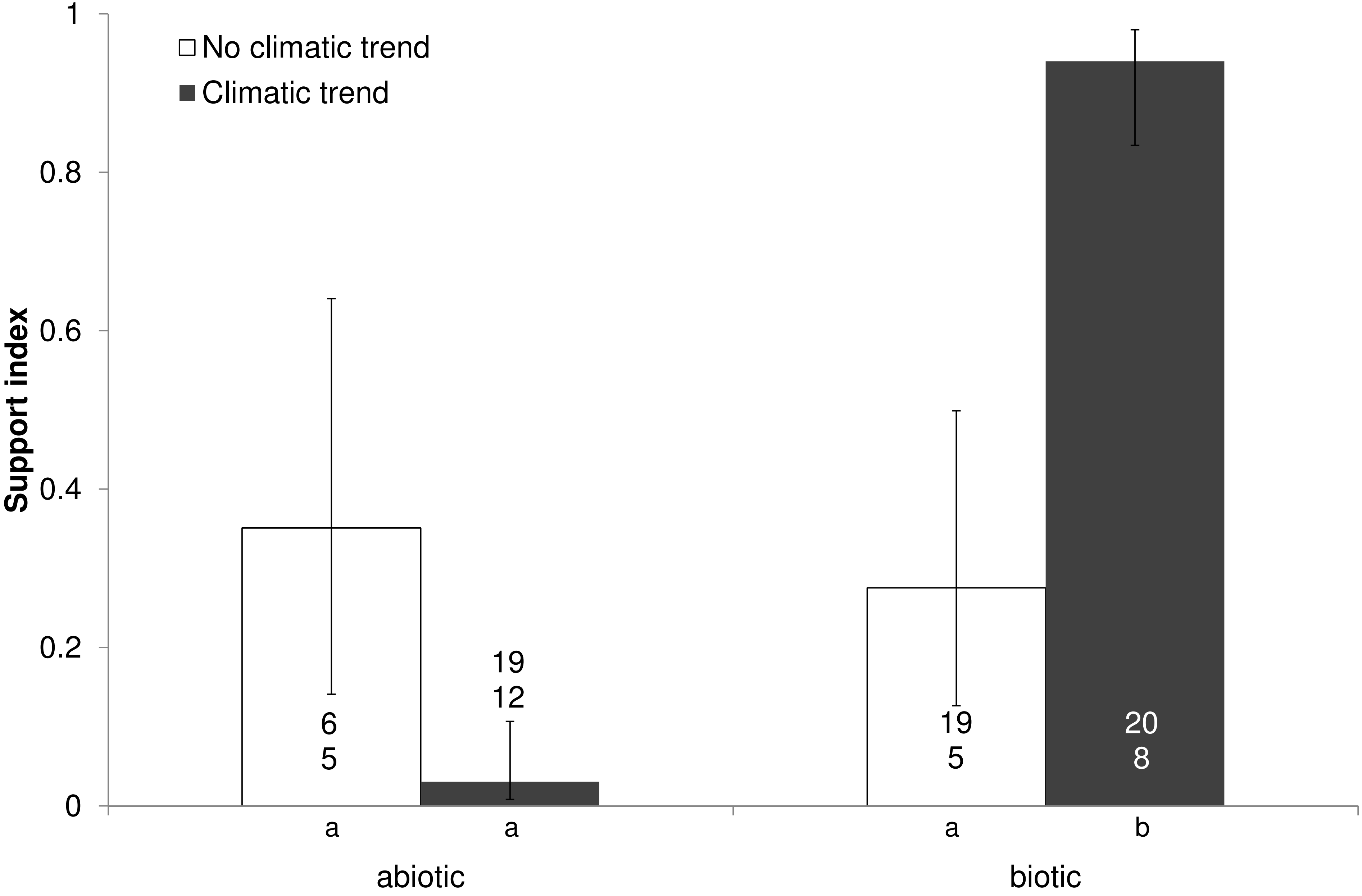

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Support index
□ abiotic
■ biotic
a
b
b
a
b
18
6
11
9
44
19
32
23
44
16
producer
primary consumer
higher consumer

Figure 4



Support index
1
0.8
0.6
0.4
0.2
0
☐ No climatic trend
■ Climatic trend
6
5
19
12
19
5
20
8
a
a
a
b
abiotic
biotic

Appendix S1 Details of studies used in analysis

Authors	**Ecosystem**	**Duration (years)**	**Taxonomic grouping**	**Mechanism category**	**Specific mechanism**	**Biotic / Abiotic**
Aanes *et al*. 2002	Terrestrial	21	Mammal	Changes in resource availability	Change in food availability	Biotic
Adamík & Král 2008	Terrestrial	26	Bird	Changes in predation interactions	Change in predator populations	Biotic
Ahola *et al*. 2009	Terrestrial	56	Bird	Changes in phenology	Change in breeding phenology	Abiotic
Anders & Post 2006	Terrestrial	37	Bird	Changes in resource availability	Change in food availability	Biotic
Bender & Weisenberger 2005	Terrestrial	36	Mammal	Changes in resource availability	Change in food availability	Biotic
Brodie & Post 2010	Terrestrial	26	Mammal	Changes in resource availability	Change in foraging efficiency	Abiotic
Cattadori *et al*. 2005	Terrestrial	155	Bird	Changes in pathogen populations		Biotic
Chase *et al*. 2005	Terrestrial	21	Bird	Changes in phenology Changes in predation interactions	Change in breeding season length Change in predation risk	Abiotic Biotic
Conner *et al*. 2005	Terrestrial	20	Bird	Changes in resource availability	Change in foraging efficiency	Abiotic
Coughenour & Singer 1996	Terrestrial	23	Mammal	Changes in resource availability	Change in food availability	Biotic
Dunham *et al*. 2011	Terrestrial	20	Mammal	Changes in resource availability Direct impacts of too much or too little water	Change in food availability Desiccation / drought stress	Biotic Abiotic
Dyrcz & Halupka 2009	Terrestrial	38	Bird	Changes in phenology Changes in phenology	Change in breeding season length Change in breeding season phenology	Abiotic Abiotic
Falls *et al*. 2007	Terrestrial	36	Mammal	Changes in resource availability	Change in food availability	Biotic
Gerten & Adrian 2002	Terrestrial	20	Invertebrate	Changes in phenology Direct impact on organism's growth or development rate	Change in breeding season length	Abiotic Abiotic
Gilbert & Raedeke 2004	Terrestrial	20	Mammal	Direct impacts of temperature	Energetic costs	Abiotic
Glenn *et al*. 2011a	Terrestrial	21	Bird	Changes in resource availability Direct impacts of temperature	Change in food availability Cold-related mortality	Biotic Abiotic
Glenn *et al*. 2011b	Terrestrial	21	Bird	Changes in resource availability	Change in food availability	Biotic
Grau & Veblen 2000	Terrestrial	95	Plant	Changes in habitat extent		Abiotic
Hari *et al*. 2006	Freshwater	25	Fish	Direct impact on organism's growth or development rate Changes in pathogen populations		Abiotic Biotic

Hersteinsson *et al*. 2009	Terrestrial	27	Mammal	Changes in resource availability	Change in food availability	Biotic
Hone & Clutton-Brock 2007	Terrestrial	27	Mammal	Changes in resource availability	Change in food availability	Biotic
Hušek & Adamík 2008	Terrestrial	41	Bird	Changes in phenology	Change in breeding phenology	Abiotic
Jovani & Tella 2004	Terrestrial	23	Bird	Direct impacts of temperature	Energetic costs	Abiotic
Kelsall *et al*. 2004	Terrestrial	81	Plant	Direct impacts of temperature	Cold-related mortality	Abiotic
				Direct impacts of too much or too little water	Desiccation / drought stress	Abiotic
Klaus 2007	Terrestrial	32	Bird	Changes in resource availability	Change in food availability	Biotic
Klvana *et al*. 2004	Terrestrial	132	Mammal	Direct impacts of temperature	Energetic costs	Abiotic
				Changes in resource availability	Change in food availability	Biotic
Kullman 2007	Terrestrial	32	Plant	Direct impacts of temperature	Cold-related mortality	Abiotic
Laaksonen *et al*. 2006	Terrestrial	59	Bird	Changes in phenology	Change in breeding phenology	Abiotic
Lewellen & Vessey 1998	Terrestrial	23	Mammal	Direct impacts of temperature	Cold-related mortality	Abiotic
Lima *et al*. 2008	Terrestrial	23	Mammal	Changes in resource availability	Change in food availability	Biotic
Macdonald *et al*. 2010	Terrestrial	21	Mammal	Changes in resource availability	Change in food availability	Biotic
				Changes in pathogen populations		Biotic
				Changes in human-related mortality		Biotic
Magnusson *et al*. 2010	Terrestrial	22	Mammal	Changes in habitat extent		Abiotic
Manca & DeMott 2009	Freshwater	22	Invertebrate	Changes in predation interactions	Change in predation risk	Biotic
Martin 2007	Terrestrial	20	Plant	Changes in predation interactions	Change in predator population	Biotic
			Bird	Changes in predation interactions	Change in predation risk	Biotic
Matthysen *et al*. 2011	Terrestrial	29	Bird	Changes in phenology	Change in breeding phenology	Abiotic
McGrath & Lorenzen 2010	Freshwater	22	Amphibian	Direct impact on organism's growth or development rate		Abiotic
				Changes in habitat extent		Abiotic
McLaughlin *et al*. 2002	Terrestrial	38	Invertebrate	Changes in phenology	Loss of interactions due to phenological mismatch	Biotic
Morrissette *et al*. 2010	Terrestrial	30	Bird	Changes in resource availability	Change in food availability	Biotic
				Changes in phenology	Loss of interactions due to phenological mismatch	Biotic
Murray *et al*. 2006	Terrestrial	40	Mammal	Direct impacts of temperature	Heat stress	Abiotic
Nevoux *et al*. 2008	Terrestrial	22	Bird	Changes in resource availability	Change in food availability	Biotic

Ogutu & Owen-Smith 2005	Terrestrial	32	Mammal	Changes in resource availability Changes in predation interactions	Change in food availability Change in predation risk	Biotic Biotic
Parker 1993	Terrestrial	54	Plant	Direct impacts of too much or too little water Direct impacts of temperature	Desiccation / drought stress Cold-related mortality	Abiotic Abiotic
Peach *et al*. 1995	Terrestrial	21	Bird	Direct impacts of temperature	Cold-related mortality	Abiotic
Pearce-Higgins *et al*. 2009	Terrestrial	28	Bird	Changes in phenology	Change in breeding phenology	Abiotic
Pearce-Higgins *et al*. 2010	Terrestrial	34	Bird	Changes in resource availability Changes in phenology Direct impacts of temperature	Change in food availability Loss of interactions due to phonological mismatch Cold-related mortality	Biotic Biotic Abiotic
Pérez-Ramos *et al*. 2010	Terrestrial	26	Plant	Direct impacts of too much or too little water	Desiccation / drought stress	Abiotic
Piovesan & Adams 2001	Terrestrial	105	Plant	Direct impacts of too much or too little water	Desiccation / drought stress	Abiotic
Post & Stenseth 1999	Terrestrial	20	Mammal	Changes in resource availability	Change in food availability	Biotic
Potti 2009	Terrestrial	24	Bird	Changes in phenology	Change in breeding phenology	Abiotic
Pucek *et al*. 1993	Terrestrial	21	Mammal	Changes in resource availability	Change in food availability	Biotic
Reading 2007	Freshwater	23	Amphibian	Direct impacts of temperature	Energetic costs	Abiotic
Rehmeier *et al*. 2005	Terrestrial	20	Mammal	Changes in resource availability	Change in food availability	Biotic
Robinson *et al*. 2004	Terrestrial	37	Bird	Changes in resource availability	Change in food availability	Biotic
Schwartz & Armitage 2005	Terrestrial	29	Mammal	Changes in resource availability Changes in resource availability	Change in food availability Change in foraging efficiency	Biotic Abiotic
Selås 2001	Terrestrial	65	Bird	Changes in resource availability	Change in food availability	Biotic
Shone *et al*. 2006	Terrestrial	34	Invertebrate	Direct impact on organism’s growth or development rate		Abiotic
Solberg *et al*. 2001	Terrestrial	21	Mammal	Changes in resource availability Changes in resource availability	Change in food availability Change in foraging efficiency	Biotic Abiotic
Sumacki & Stepniewski 2007	Terrestrial	20	Bird	Changes in phenology	Change in breeding season length	Abiotic
Suski & Ridgway 2007	Freshwater	22	Fish	Changes in phenology	Change in breeding phenology	Abiotic
Tratalos *et al*. 2010	Terrestrial	58	Invertebrate	Changes in resource availability Direct impacts of too much or too	Change in food availability Desiccation / drought stress	Biotic Abiotic

				little water		
Visser *et al*. 2006	Terrestrial	20	Bird	Changes in phenology	Loss of interactions due to phonological mismatch	Biotic
Vucetich & Peterson 2004	Terrestrial	40	Mammal	Changes in resource availability Changes in resource availability Direct impacts of temperature	Change in food availability Change in foraging efficiency Energetic costs	Biotic Abiotic Abiotic
Watson *et al*. 1998	Terrestrial	53	Bird	Changes in phenology	Change in breeding phenology	Abiotic
Winkler *et al*. 2002	Terrestrial	21	Bird	Changes in phenology	Change in breeding phenology	Abiotic

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Appendix S2 Results of analysis using full data set, including papers where evidence for mechanism was absent or based on a species other than the focal species.

Analyses were also performed using the full set of studies returned after the literature search and screening, including studies where there was no evidence for the mechanism or the evidence for the mechanism was based on a different species. These gave results qualitatively similar to those presented in the main paper, where mechanisms were only included if they were based on evidence from the same species. Duration was found to be a significant predictor of mechanism importance in this dataset and was therefore retained in all analyses.

There was a significant difference in support between biotic and abiotic mechanisms ($F_{1,\,184} = 5.2$, $P = 0.02$), with biotic mechanisms more frequently supported than abiotic ones. Although there was not significant variation in the level of support for different categories of mechanism overall ($F_{6,\,175} = 1.1$, $P = 0.37$), there was a tendency for mechanisms relating to resource availability and predation to be supported more than those related to direct impacts of water stress (Fig. S1).

There was no significant effect of latitude ($F_{5,\,167} = 0.93$, $P = 0.47$; $F_{1,\,182} = 0.01$, $P = 0.90$), ecosystem ($F_{5,\,167} = 0.32$, $P = 0.90$; $F_{1,\,180} = 0.05$, $P = 0.82$), thermal strategy ($F_{5,\,165} = 0.76$, $P = 0.58$; $F_{1,\,179} = 0.08$, $P = 0.78$) or taxonomic grouping (model did not converge; $F_{3,\,172} = 1.4$, $P = 0.25$) on the relative importance of different mechanism types, or biotic versus abiotic mechanisms respectively. There was a significant difference in the support for biotic versus abiotic mechanisms between primary and higher consumers, driven by the low level of support for abiotic processes amongst higher consumers ($F_{1,\,153} = 4.1$, $P = 0.04$; Fig. S2).

The relative importance of biotic and abiotic mechanisms again varied with the direction of the relationship between precipitation and population metrics, with biotic mechanisms being more likely to show a positive effect of precipitation than abiotic mechanisms ($F_{1,58} = 8.5$, $P = 0.005$). There was no difference in the frequency of positive and negative relationships with temperature between abiotic and biotic factors in the full dataset ($F_{1,38} = 2.6$, $P = 0.12$).

The interaction term testing whether there was a difference in the importance of biotic and abiotic mechanisms between studies that reported a trend in climate over the study period versus those without a trend, remained significant when analysed across this full dataset ($F_{1,73} = 10.02$, $P = 0.002$). Biotic factors appeared more important than abiotic factors in studies with a significant climatic trend, whilst in the absence of such a trend abiotic factors appeared to be more important (Fig. S3).

Figure S1. Mean support index ± se (proportion of population time series for which a mechanism is supported) for each mechanism category. Biotic mechanisms are in black, abiotic in white and mixed categories in grey. Data are derived from all studies, irrespective of the level of support for a mechanism. Labels on each column show the number of tests carried out (top number) and the number of studies from which the tests were drawn (bottom number). Letters link columns that do not differ significantly ($P > 0.05$); columns of bars with all non-matching letters therefore differ significantly ($P < 0.05$).

Figure S2. Mean support index ± se (proportion of population time series for which a mechanism is supported) for abiotic (white) and biotic (black) mechanisms across different trophic levels). Data are derived from all studies, irrespective of the level of support for a mechanism. Biotic mechanisms are more frequently supported than abiotic factors and the relative importance of the two mechanism types varies with species' trophic level. Labels on each column show the number of tests carried out (top number) and the number of studies from which the tests were drawn (bottom number). Letters link columns that do not differ significantly ($P > 0.05$); columns of bars with all non-matching letters therefore differ significantly ($P < 0.05$).

Figure S3. Mean support index ± se (proportion of population time series for which a mechanism is supported) for abiotic and biotic mechanisms between studies that document a climatic trend (black) and those that do not (white). Data are derived from all studies, irrespective of the level of support for a mechanism. Labels on each column show the number of tests carried out (top number) and the number of studies from which the tests were drawn (bottom number). Some studies are represented in more than one column. Letters link columns that do not differ significantly ($P > 0.05$); columns of bars with all non-matching letters therefore differ significantly ($P < 0.05$).

Figure S1

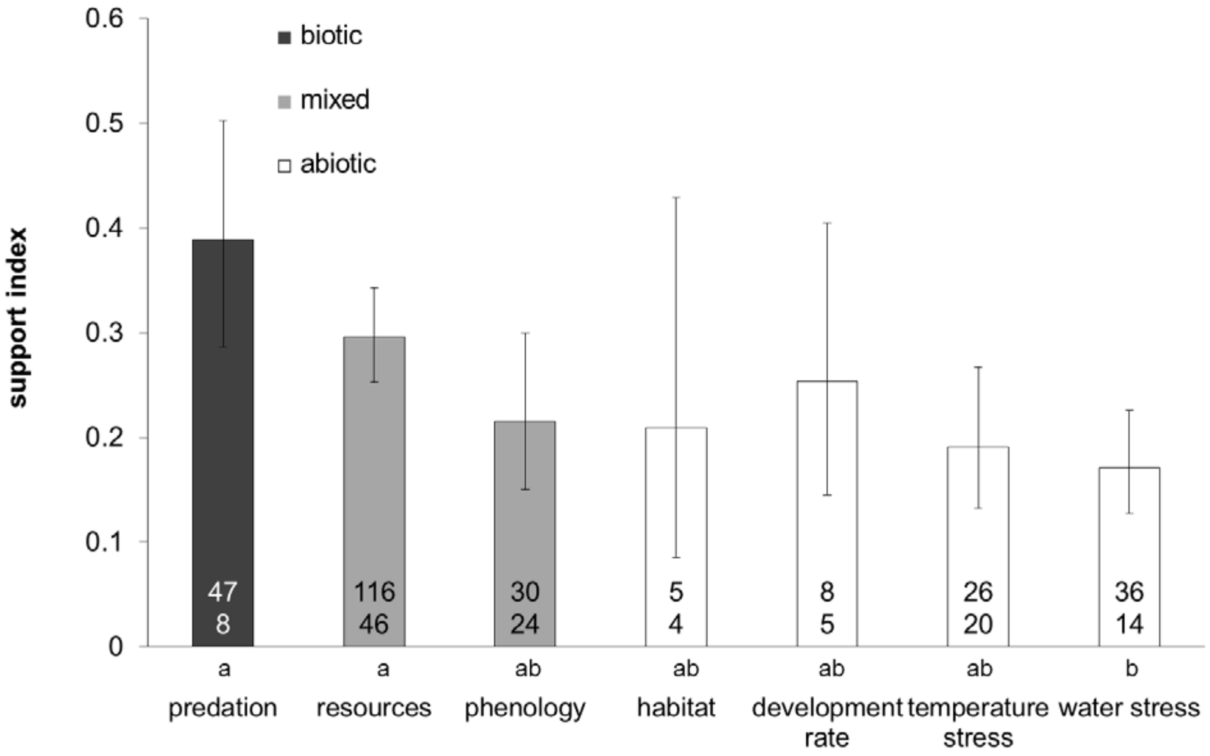
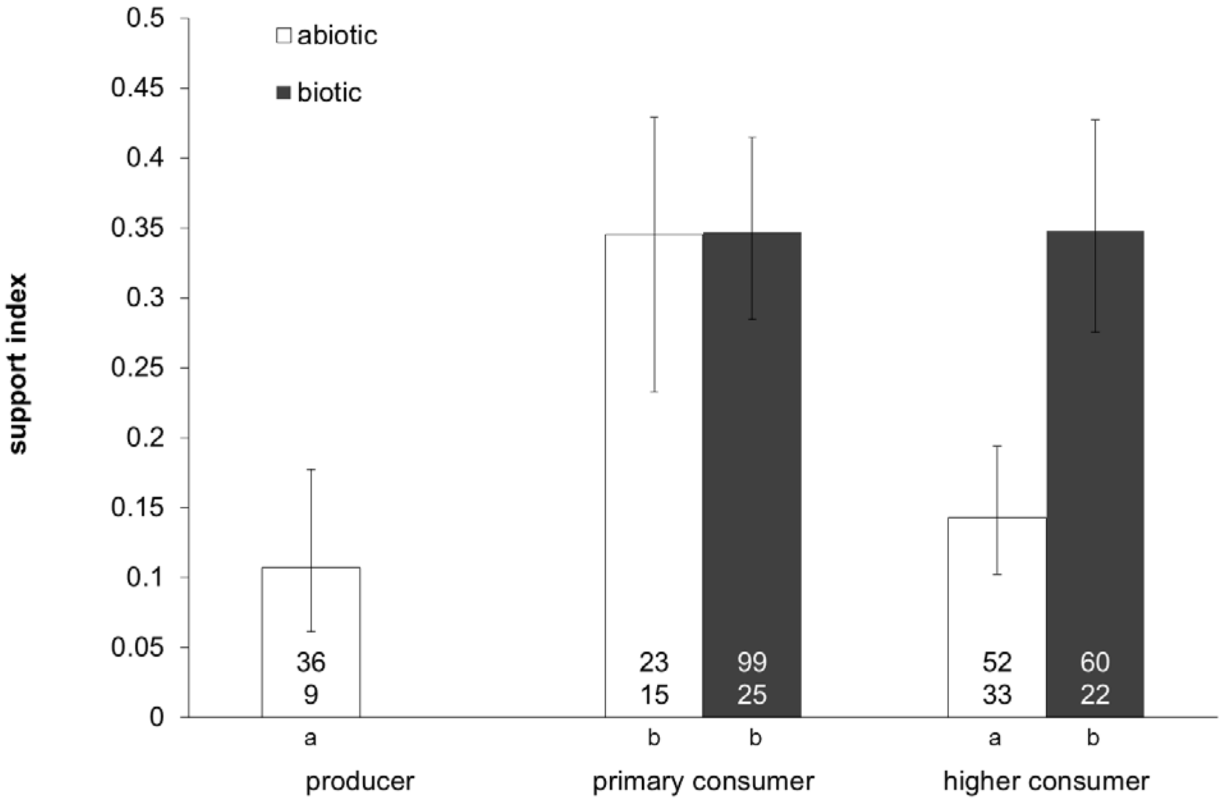
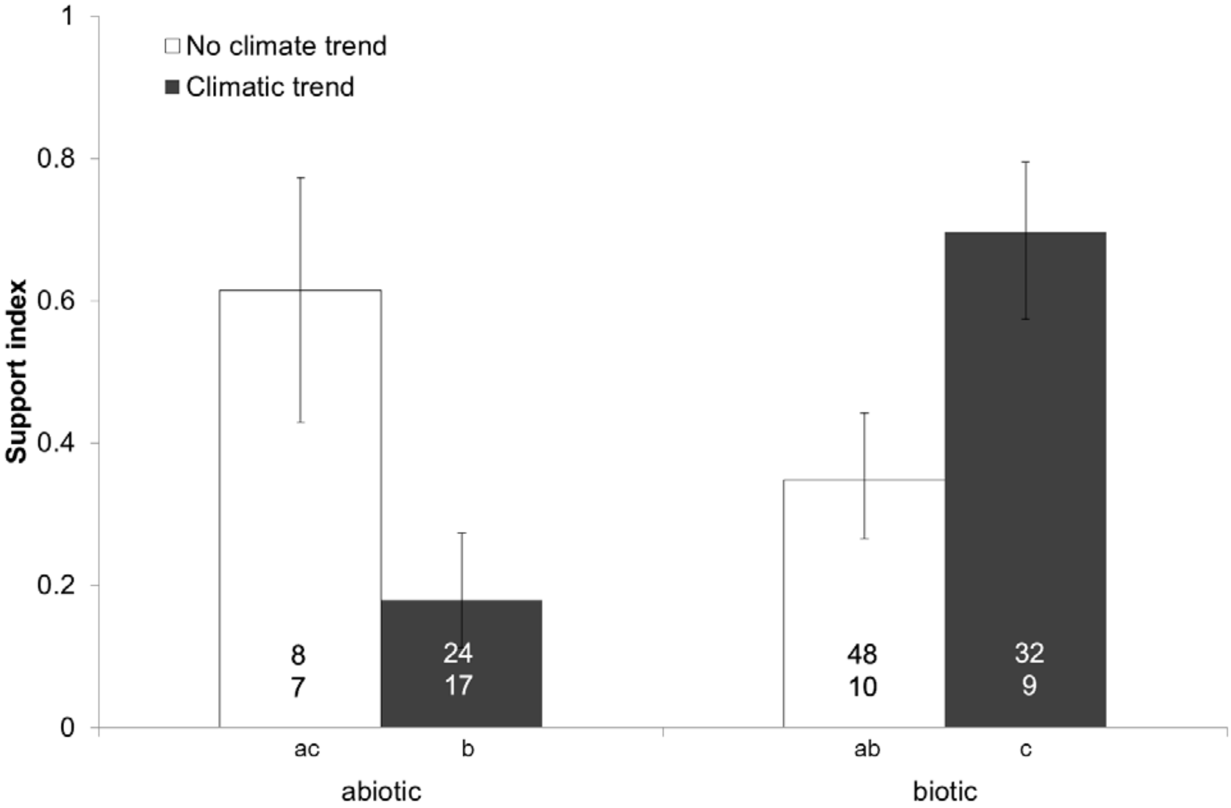

0.6
0.5
0.4
0.3
0.2
0.1
0
support index
■ biotic
■ mixed
□ abiotic
47
8
116
46
30
24
5
4
8
5
26
20
36
14
a
a
ab
ab
ab
ab
b
predation
resources
phenology
habitat
development rate
temperature stress
water stress

Figure S2



□ abiotic
■ biotic
support index
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
36
9
23
15
99
25
52
33
60
22
a
b
b
a
b
producer
primary consumer
higher consumer

Figure S3



1
0.8
0.6
0.4
0.2
0
Support index
□ No climate trend
■ Climatic trend
8
7
24
17
48
10
32
9
ac
b
ab
c
abiotic
biotic