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REVIEW AND SYNTHESIS

Means and extremes: building variability into community-level climate change experiments

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Abstract

Experimental studies assessing climatic effects on ecological communities have typically applied static warming treatments. Although these studies have been informative, they have usually failed to incorporate either current or predicted future, patterns of variability. Future climates are likely to include extreme events which have greater impacts on ecological systems than changes in means alone. Here, we review the studies which have used experiments to assess impacts of temperature on marine, freshwater and terrestrial communities, and classify them into a set of 'generations' based on how they incorporate variability. The majority of studies have failed to incorporate extreme events. In terrestrial ecosystems in particular, experimental treatments have reduced temperature variability, when most climate models predict increased variability. Marine studies have tended to not concentrate on changes in variability, likely in part because the thermal mass of oceans will moderate variation. In freshwaters, climate change experiments have a much shorter history than in the other ecosystems, and have tended to take a relatively simple approach. We propose a new 'generation' of climate change experiments using down-scaled climate models which incorporate predicted changes in climatic variability, and describe a process for generating data which can be applied as experimental climate change treatments.

Keywords

climate change, down-scaled climate models, experimental treatments, experiments, freshwater, marine, terrestrial, weather scenarios.

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INTRODUCTION

Predicting the consequences of climate change requires an understanding of the complex physiological, ecological and evolutionary processes which underpin the relationships between climate and biodiversity (Lavergne *et al.* 2010; Bellard *et al.* 2012). Our understanding of the effects of changing climate on ecosystems has been greatly informed by field studies showing range shifts (including invasions) (e.g. Parmesan 2006; Thomas 2010; Dietl & Flessa 2011), altered patterns of phenology (e.g. Walther 2004; Parmesan 2006; Pau *et al.* 2011), changes in body size distributions (e.g. Sheridan & Bickford 2011; Goodman *et al.* 2012) and altered rates of ecosystem functions (e.g. Traill *et al.* 2010). Palaeoecological and long-term ecological data also provide important context for the study of changing climates (e.g. Dietl & Flessa 2011; Willis & MacDonald 2011). Although we have an increasingly complete view of the effects of climate change on populations and individual physiology, it remains a challenge to understand the effects on biotic interactions and ecological feedbacks (Traill *et al.* 2010; Van der Putten *et al.* 2010; Walther 2010). Such an understanding is critical if we are to apply our predictions of climate change effects to core issues such as conservation planning (McCarty 2001).

Climate change across much of the planet will include underlying increases in mean meteorological quantities (e.g. temperature, precipitation, solar radiation and wind) ('trend effects'; Jentsch *et al.* 2007), but also the variability of these quantities. It is becoming clear both from climate modelling and from trends in climate, that future climate will be characterised in many regions by increases in the frequency of extreme events such as heat waves and dry spells ('event effects'; Jentsch *et al.* 2007) (Katz & Brown 1992; Easterling *et al.* 2000; IPCC 2012). We have used the IPCC (2012) definition of extreme events which is essentially statistical (i.e. events which fall outside the 90th percentile under current climatic conditions). Extreme high temperature events include increases in intensity (higher maximum temperatures), frequency and duration of high temperature events which are rare under current climatic conditions (IPCC 2012). We know that in many ecological systems extremes are the most important events for determining community dynamics (Gutschick & BassiriRad 2003). The probability and consequences of extreme events have been increasingly discussed in the scientific literature, particularly in the context of climate change (Jentsch *et al.*

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2007). However, biological responses to temperature can be highly nonlinear and are typified by thresholds, interactions with other climatic conditions, such as rainfall, and the potential for organisms to adapt to changed conditions (Gutschick & BassiriRad 2003; Benedetti-Cecchi *et al.* 2006).

There is an increasing awareness of the need for experimental approaches to studying climate change, ideally embedded in a framework which also incorporates paleoecological and evolutionary data, field studies and computational modelling (Dawson *et al.* 2011). Although the use of latitudinal and altitudinal gradients as surrogates for experimental climate change treatments is highly informative (e.g. Umina *et al.* 2005) variation in conditions along those gradients may not accurately reflect predicted changes in climate, particularly with respect to frequency of extreme climatic events. Experimentally applying climate change treatments is one way to understand the effects of variability and extreme weather events on ecological systems.

Experiments have been increasingly used over the last few decades to understand climate change impacts, and in particular, the mechanisms that underlie them. These have included experiments where CO_2 and temperature have been manipulated at the scale of whole trees (Crous *et al.* 2012), warming of sections of Arctic tundra (Henry & Molau 1997), and using heating cables to warm forest soils (Melillo *et al.* 2002). Generally, these studies have investigated the effects of mean warming rather than any change in underlying variability. However, increases in climate variability and frequency of extreme events are likely to be biologically more significant. Predicted increases in mean temperatures due to climate change are likely to impact species over relatively long time periods (years to decades), resulting in range shifts and alterations in ecological interactions (Parmesan 2006). Extreme disturbances of various types are associated with dramatic biological effects at different levels of ecological organisation, from the individual (e.g. physiological stress) (Parmesan *et al.* 2000) to the ecosystem (shifts between states) (Allen & Breshears 1998; Scheffer & Carpenter 2003). Although mean trend effects may be moderated by evolutionary change (Sgro *et al.* 2011), event effects are likely to have immediate consequences which may result in extinction even when there is potential for evolutionary change (Gutschick & BassiriRad 2003).

In the following review, we assess the ways in which conditions resulting from climate change predictions have been applied as treatments in experiments on freshwater, marine and terrestrial systems. We assess the approaches taken in the different ecosystem types and the basis for those differences. Finally, we describe an approach to using regional or global climate change models as the basis for generating experimental treatments which reflect the complex features of predicted future weather conditions.

DISCUSSION

Part one: trends and insights from climate change experiments

Studies which have experimentally applied temperature treatments to ecological communities in the period 2000–2012 were reviewed using Web of Science (accessed 1 July 2012 to 1 November 2012, using the keywords climate change with; experiment or experimental or manipulation or warming). Studies which used natural gradients such as altitude and latitude were deliberately excluded, as they do not directly manipulate environmental conditions. We also excluded studies of single species, which includes a large body of literature from studies of adaptive capacity to evolutionary genetics. Because there were relatively few freshwater studies, the literature review was extended for freshwaters only to include the time period 1995–2012. This resulted in 110 studies (Supplementary materials S1), 66 from terrestrial environments, 23 from marine settings and 21 from freshwaters. Those studies were classified into *a priori* defined 'generations' of experiments, each of which treats temperature in different ways (Table 1).

Generation one: fixed mean experiments

Fixed mean experiments represent the simplest treatment possible and apply temperature treatments at a stable level over the length of the experiment. Most often these take the mean temperature of current conditions and add an increment to it to generate a new mean temperature, which is then applied as the treatment (compare Fig. 1a,b). Some of the studies listed in Table 1 (e.g. Beisner *et al.* 1996; Mitchell & Lampert 2000) compared fixed temperature treatments, others (e.g. Petchey *et al.* 1999; Fox & Morin 2001) compared a constant to a warming treatment. These types of experiments underestimate the effects of climate change as they do not include the 'event effect' component in the treatment. The warming treatments in these experiments are also associated with a reduction in temperature variability, potentially confounding any results.

Generation two: fixed minima experiments

Fixed minima or maxima experiments have commonly been applied in warming experiments in the field. Experiments using substrate warmers inserted into the forest floor are an example of this type of approach (Melillo *et al.* 2002), as are experiments which re-radiate heat during the night to reduce night time minimum temperatures (e.g. Lloret *et al.* 2005). While able to prevent the coolest temperatures occurring, and having some warming effects on cool to moderate temperature days, this approach cannot affect the warmest days or generate high temperature extremes. Effectively, these

Table 1 Review and classification into generations of community climate change experiments 2000–2012 (terrestrial and marine) and 1995–2012 (freshwater) which involved temperature manipulations (excluding other physical and chemical manipulations). For definitions of the 'generations' of studies, see the main text. A number of studies (with percentages of the total in brackets following) are shown. Individual papers are shown in Table S1

				Number of studies found		
Generation	Effects on mean	Effects on variability	Incorporates extreme events?	Terrestrial	Marine	Freshwater
Fixed mean	Increase	Large reduction	No	3 (4.5%)	15 (65.2%)	5 (23.8%)
Fixed minima	Increase	Small reduction	No	7 (10.6%)	0 (0%)	0 (0%)
Fixed increment	Increase	No effect	Some	52 (78.8%)	8 (34.8%)	15 (71.4%)
Extreme event studies	Increase	Increase	Yes	4 (6.1%)	0 (0%)	1(4.8%)

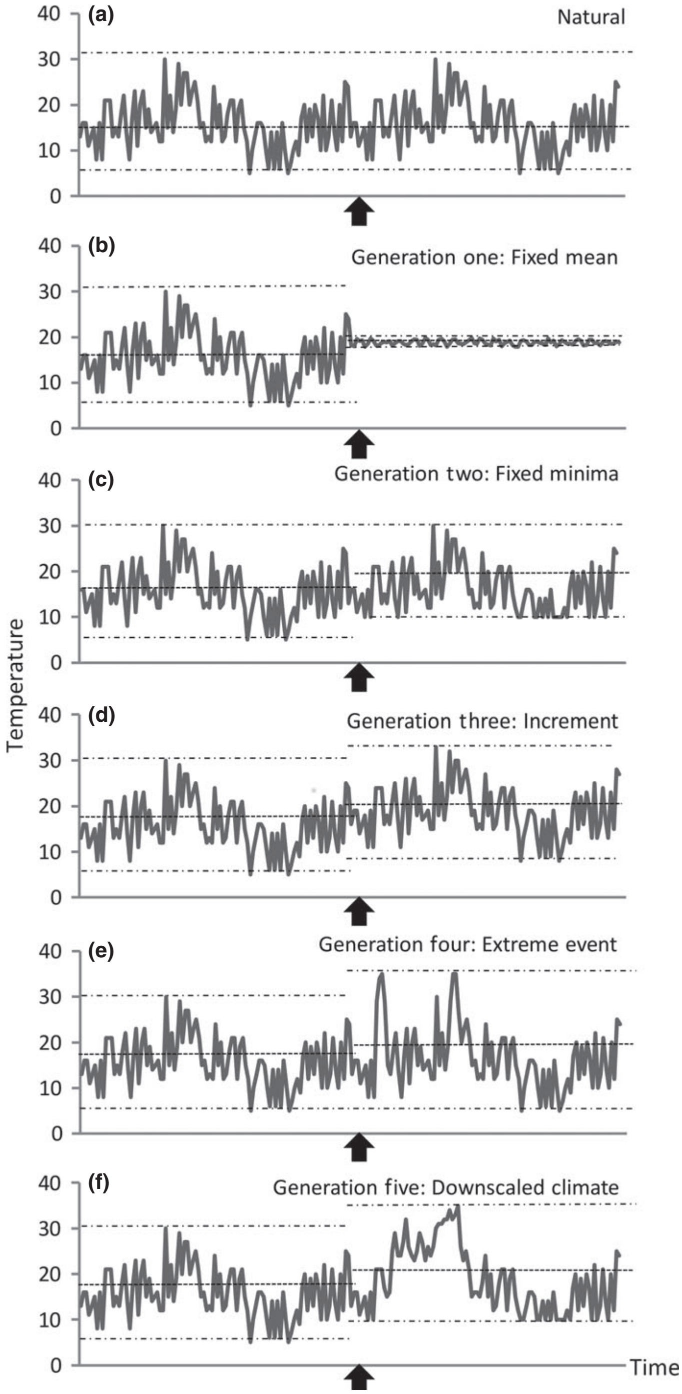

Figure 1 Conceptual diagram of generations of temperature treatments used in climate change experiments. (a) baseline temperature (natural or current scenario), (b) fixed mean (temperature set to a fixed value), (c) fixed minima (temperature has a fixed minimum), (d) increment (fixed increment is applied to natural variability), (e) extreme event (extreme event is superimposed on natural variability), (f) down-scaled climate model (temperature is determined by weather scenarios generated from down-scaled climate model). Dashed lines indicate maximum, mean and minimum temperatures. The black arrow indicates when experimental treatments are applied.

treatments generate fixed minimum temperatures. The effect is to increase mean temperatures but to reduce variability, although not to the extent of fixed mean experiments (Fig. 1c).

Generation three: increment studies

Increment studies apply a temperature treatment while retaining natural variability in temperature. Most often, these treatments are applied as a fixed increment (for example, + 3.5 °C) over natural conditions. These experiments have the advantage that they incorporate many of the natural features of weather, for example, one warmer than average day is more likely to follow another than it is to follow a colder than average day. Overall, these studies increase mean temperatures while retaining the variability which is typical of current climates (Fig. 1d). For example, Yvon-Durocher *et al.* (2010) used twenty mesocosms in southern England and warmed ten of these by 3–5 °C above ambient conditions. Similarly, Perdomo *et al.* (2012) applied a 6 °C increment to moss patches in the field. These types of experiments cannot incorporate features such as predicted climates where, for example, winter becomes warmer but spring becomes cooler. Nor do these kinds of experiments take into account changes in the climate variability. As such, they may underestimate the effects of climate change in some systems.

Generation four: extreme event studies

The most recent examples of climate change studies explicitly include extreme events in some fashion. In terrestrial studies, experimental enclosures have been exposed to drought, night heat waves and extreme rainfall scenarios to assess effects on primary productivity (e.g. Fay *et al.* 2000; Beier *et al.* 2004). These approaches do not seem to have been applied in freshwater studies of the effects of temperature. Dang *et al.* (2009) applied an increased diel temperature variation to stream mesocosms and assessed impacts on detrital decomposition, but this experiment exposed the system to a cyclic series of extreme events rather than periodic events. A number of freshwater studies have assessed the effects of drying as an extreme event (Leberfinger *et al.* 2010; Ledger *et al.* 2011), but none to date have considered extreme temperature events such as heat waves explicitly, as shown in Figure 1e. Extreme event studies increase means and variability in temperatures, but do not replicate changes in the timing or duration of extreme events.

Part two: comparing approaches across ecosystems

Terrestrial ecosystems

Terrestrial studies are by far the most common in the literature, with 60% of reviewed studies being terrestrial, despite the shorter time period which was considered for the literature review. Climate change experiments in terrestrial settings have tended to consider the effects of not only temperature but also rainfall and increased atmospheric CO_2 concentrations (the latter two are not considered in this review). Smaller scale experiments in terrestrial settings have utilised chambers and have applied temperature treatments as both fixed means and fixed increments. Larger scale terrestrial experiments utilising substrate warmers, in particular, were a feature of early high-profile climate change research (Melillo *et al.* 2002). These approaches logistically lend themselves to fixed increment treatments, and these predominate in the published terrestrial climate change literature (Table 1). Although there has been recognition for some years of the need to incorporate extreme events into studies of climate change impacts on terrestrial ecosystems (Jentsch *et al.* 2007), these continue to be the exception in studies of the effects of temperature (Table 1). That said, a number of recent studies have explored the impacts of extreme heat events either in isolation, or in combination with other stressors (Van Peer *et al.* 2004; Bjerke *et al.* 2011; Perdomo *et al.* 2012). Combined treatments are particularly relevant to terrestrial systems, where high temperatures are strongly associated with reduced rainfall, and for plant communities, where high rainfall can mitigate impacts of high temperatures (Van Peer *et al.* 2004).

Marine ecosystems

Studies of the effects of climate change-induced changes in temperature on marine communities remain relatively rare, in part because of the logistic difficulties of applying treatments at large scales. Marine climate change studies have included an emphasis on the effects of CO_2 and acidification, as key impacts on coral reefs (Hoegh-Guldberg *et al.* 2011) and pelagic primary producers (Beardall *et al.* 2009). The majority of experimental studies of the impacts of increased temperatures have either been fixed mean studies or fixed increment studies (Table 1). For the majority of marine systems this may make sense, as the high thermal mass of the oceans means that warming will tend to occur relatively slowly (days to weeks), making oceanic systems more tolerant of short-term (days) spikes in atmospheric temperatures. While extreme events may be proportionally less important in terms of temperature impacts in marine settings, there are clearly described impacts of relatively short term (weeks) warming episodes on coral reefs (Baker *et al.* 2008). It may be that the emphasis on field studies of climate change impacts, and the difficulties of carrying out scalable experiments on these systems has led to the relative paucity of experimental warming studies on marine communities.

Freshwater ecosystems

In freshwater systems, a number of recent reviews have discussed the potential impacts of climate change at scales from regional (e.g. Heino *et al.* 2009; Johnson *et al.* 2009; Fenoglio *et al.* 2010; Morrongiello *et al.* 2011) to global (e.g. Ficke *et al.* 2007; Perkins *et al.* 2010; Woodward *et al.* 2010). Freshwater systems are particularly vulnerable to changing climates as they are often highly range-restricted, and are subject to competition for water resources with human uses (Hobday & Lough 2011). Effects of extreme events in freshwater occur in two main areas. The first is via extreme heat events, which in aquatic systems also have consequences for the availability of oxygen and concentrations of toxicants (Ficke *et al.* 2007). Second, extreme rainfall events can have major effects on disturbance regimes via changed hydrology (Ficke *et al.* 2007). These effects become more complex in areas where seasonality of rainfall is predicted to change under climate change scenarios, or where changes in human water demands further impact water availability (Kundzewicz *et al.* 2008).

Direct effects of increased stream temperatures are predicted to have major implications for the distribution of cold water fish, particularly salmonids (Meisner 1990; Bryant 2009). Ecosystem consequences of altered climate are predicted to include changes in palatability of food resources (van de Waal *et al.* 2010; Sardans *et al.* 2012), size spectra of animals (Yvon-Durocher *et al.* 2011) resulting in altered food-web structure (Woodward *et al.* 2010). These studies by-and-large have been based on field studies or are conceptual in nature, although in recent years there has been a small number of experimental studies (e.g. Yvon-Durocher *et al.* 2011; Dossena *et al.* 2012). The studies have predominantly considered temperature effects as either increases to a fixed mean or fixed increment studies (Table 1). In larger water bodies, the high thermal mass of aquatic systems may make them less vulnerable to short-term heat extremes, but in many shallow water bodies, short-term heat waves may have profound effects (Dokulil *et al.* 2010). The most recent climate change experiments in freshwaters have included extreme events as one-off or recurring events (Leberfinger *et al.* 2010; Ledger *et al.* 2011). These studies have shown that extreme events can greatly alter ecosystem functioning and food-web structure in freshwaters.

Part three: using down-scaled climate models to generate experimental climate change treatments

It is now possible to generate experimental treatments which are based on the predictions of global climate change models for large scale climate phenomena, but down-scaled to generate hourly weather scenarios. Two types of approaches (dynamical and statistical) are normally used to take information from global climate models (GCMs) (~ 100 km resolution) to be applied at higher resolutions that are more meaningful to local ecological scales (see Wilby & Wigley 1997; for a review). These approaches have been widely used in hydrology, but not directly in ecological experiments (Wilby & Dawson 2012). GCMs typically have coarse temporal (monthly) and spatial resolution and are most useful at these scales. Experimental treatments for ecological studies need predictions at relatively fine spatial and temporal scales. These need to incorporate increases in mean temperatures, but also increased variability and increased frequency of extreme events, such as heat waves and extreme rainfall events, and more subtle impacts such as changes in cloud cover. For example in Figure 1f, prolonged extreme high temperature events ('heatwaves') appear in the treatment based on predictions from a GCM.

In our example, we sought to generate a climate change treatment to apply to indoor experimental stream flumes to assess climate change impacts on temperate Australian stream benthic communities. We wanted to compare responses to conditions representative of mid-summer over the last decade, to mid-summer conditions predicted to occur under a climate change scenario for 2100. The controllable variables in the flumes were temperature, rainfall (as flow velocity) and light intensity. We carried out the down-scaling process for one future time (2100) and one time of year (60 days in summer), using a single model and one emissions scenario (A1B scenario, predicting a year 2100 carbon dioxide concentration of 700 ppm (IPCC 2000). However, more complex experiments could generate treatments for other years, times of year or emissions scenarios. In addition, multi-model ensembles could be used to capture the uncertainty in climate predictions resulting from structural differences in the GCMs as well as uncertainty due to variations in initial conditions or model parameterisation (Semenov & Stratonovitch 2010). It is important that these weather time series are not averaged in a multiple ensemble as the resultant time series will lose its statistical variation. Rather the key here is to ultimately generate multiple weather time series treatments (ensembles) that are applied experimentally so that the ecological results are robustly replicated.

Our strategy was to use the information contained in a GCM output, which projects how climate may evolve under future scenarios over the following centuries, and apply that to the local scale. We then merged this data with statistical information from real historical observations and applied that to the changed climate from the GCM to a time series at daily resolution using a 'weather generator' (see below). We used the MIROC (Model for Inderdisciplinary Research on Climate) global climate model outputs available from the Center for Climate System Research (CCSR), University of Tokyo (http://www.ccsr.u-tokyo.ac.jp/) as the basis for our generation of the temperature treatment data. The model has a spatial resolution of 1.4 degree in longitude, 0.5–1.4 degree in latitude, and 43 vertical levels in the medium-resolution version. We chose this model because it has performed well for the Australian climate (Pitman & Perkins 2008). Data were extracted from the CMIP3 (http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php) archive which is a repository for climate models that were used in preparing the IPCC Fourth Assessment Report (http://www.ipcc.ch/). We extracted the air temperature variable (TASA1) from the run 'sresb1atmmotasmiroc3_2medres' to demonstrate the method. This file was for the A1B scenario with a carbon dioxide concentration in the year 2100 of 700 ppm. Further information on climate change scenarios can be found at www.ipcc.ch/pdf/special-reports/spm/sres-en.pdf. We extracted data for the grid cell closest to Melbourne Airport, Australia (37.67 °S 144.83 °E) for the 21st century.

To generate weather data, we entered the GCM data into the LARS-WG (Long Ashton Research Station Weather Generator) stochastic weather generator (http://www.rothamsted.ac.uk/mas-models/larswg.php) (Semenov *et al.* 1998). LARS-WG is a model simulating hourly time series of daily weather at a single site, which can generate long time series of weather conditions for a particular site, and includes extreme weather events, such as extreme daily precipitation and long dry spells or heat waves (Semenov *et al.* 1998). LARS-WG has been well validated in diverse climates around the world (Semenov *et al.* 1998). It utilises semi-empirical distributions for the lengths of wet and dry day series, daily precipitation and daily solar radiation. The seasonal cycles of means and standard deviations are modelled by finite Fourier series of order three and the residuals are approximated by a normal distribution (http://www.rothamsted.ac.uk/mas-models/download/LARS-WG-Manual.pdf).

We used the following methodology as per Semenov & Stratonovitch (2010).

1 Model Calibration – Observed weather data from Melbourne airport (Australian Bureau of Meteorology site number: 086 282, elevation: 113 m, period: 1990–2009) were analysed to determine the local statistical characteristics of air temperature. This information is stored in two parameter files.

2 Model Validation – the statistical characteristics of the observed and synthetic weather data were analysed to determine if there are any statistically significant differences (none found).

3 Generation of Synthetic Weather Data – the parameter files derived from observed weather data during the model calibration process were used to generate synthetic weather data having the same statistical characteristics as the original observed data, but differing on a day-to-day basis. We applied our global climate model-derived changes in temperature to the LARS-WG parameter files to generate daily weather for 2090–2100.

4 Experimental series – A series of weather (20 years long) is generated based on the changes in global climate (2090–2100) and the January/February period for the 10th year was extracted for use in driving the experimental treatments (Fig. 2). Data were similarly generated for the control period (1990–2010). Probability distribution functions for distributions of minimum and maximum temperatures were generated for 2100 (generated by the simulation) and based on combined data for real weather data from the same region 1990–2000 (Fig. 2). Because we needed water temperature data (rather than the air temperature data generated by the model), a long-run series of historical water temperatures for the study site were used with historical air temperature data from the Melbourne

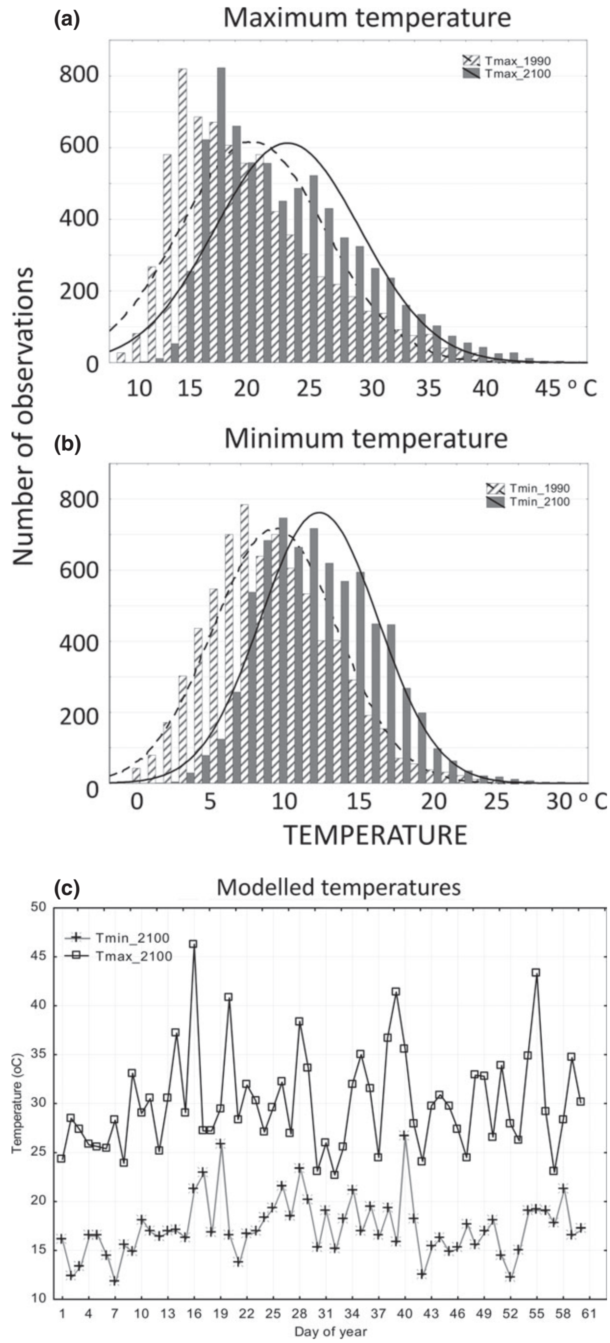

Figure 2 Example of the potential to downscale climate models to generate climate change treatments. Probability distribution functions illustrate the shifts in the actual and expected distributions of (a) maximum and (b) minimum temperatures for the decade 1990–2000 (based on real data, white striped bars) and 2100 (based on weather simulations from the climate model; grey bars). (c) Modelled temperature series for the first 60 Julian days of 2100.

airport weather station to generate a relationship between air and water temperature. It is important to note that this kind of relationships is highly nonlinear (Mohseni *et al.* 1998) and may be relatively site specific depending on local riparian vegetation and interactions with groundwater, among other factors. As such, experiments which seek to assess impacts on particular freshwater sites will require detailed historical water temperature data.

It should be noted that a stochastic weather generator is not a predictive tool that can be used in weather forecasting, but is simply a means of generating time series of synthetic weather statistically 'identical' to the observations. The resulting scenarios can be used as experimental treatments to be compared to controls resulting from ambient conditions or to treatments based on historical weather conditions. We used the variance of the 'real' historical data and applied that to the climate scenario to generate a weather series. Here, we generated a single run, as generating repeated simulations then averaging results will remove extreme events from the data.

This kind of experimental data allows the application of highly realistic treatments in experiments that include not only changes in mean conditions but also increased frequency, intensity and duration of extreme events. However, they are challenging to apply outside of highly controlled laboratory conditions. In outdoor conditions, increment studies can superimpose a warming treatment on the background conditions (e.g. Yvon-Durocher *et al.* 2010; Dossena *et al.* 2012). With simulated weather, there is the potential that a temperature treatment for a particular day may be cooler than ambient conditions, or may be considerably higher than ambient conditions. Both situations require highly energy intensive equipment to apply the treatments. Although it is possible to apply simulated weather as a treatment in an outside experiment, the approach described in the current paper is most amenable to highly controlled laboratory settings. This has the advantage that it is possible to carry out factorial designs which incorporate other stressors, which has been identified as an important next step in climate change experiments (Wernberg *et al.* 2012). These experiments require stringent attention to issues of experimental design (Jentsch *et al.* 2007; Wernberg *et al.* 2012) but have the potential to generate a much greater understanding of the interactive impacts of changing climate with other stressors.

There is a need to consider the degree to which this kind of highly controlled experiments can be scaled to large-scale real-world conditions. Previous small-scale studies have also tended to concentrate on single species, so when experimental results have not scaled to field outcomes, it is difficult to determine which of these two factors is responsible (Wernberg *et al.* 2012; Wolkovich *et al.* 2012). In plant studies, it appears that small-scale experiments may not scale up to large scales because they fail to incorporate complex community-level interactions and therefore underestimate warming impacts (Wolkovich *et al.* 2012). It is important to recognise the limitations of such small-scale experiments (Carpenter 1996; Underwood *et al.* 2005). The spatial scale of experiments has been shown to affect the magnitude of responses to treatments in a number of difference systems (see Englund & Cooper 2003 for a review). In particular, open systems that are strongly reliant on landscape-scale processes such as meta-population dynamics may respond differently to changing climate than do systems where local processes predominate (Underwood *et al.* 2005). Notwithstanding those concerns, manipulations at relatively small scales are likely to be the only way to explore impacts of climate change in a way which incorporates all of the features of predicated future climates (Englund & Cooper 2003). We propose that a suite of approaches including laboratory experiments, use of extreme events within traditional experimental increment studies and field studies of extreme events will be needed to gain a thorough understanding of the likely effects of future climates. Increasingly, frameworks are being suggested for how best to integrate across this suite of data (Denny & Benedetti-Cecchi 2012).

CONCLUSION

The majority of studies have concentrated on increases in mean temperatures, but there is an increasing awareness that extreme climatic events are likely to be the dominant force structuring ecological communities (Lloret *et al.* 2012). The need to include extreme events in climate change experiments has been well recognised over the last decade (e.g. Easterling *et al.* 2000; Jentsch *et al.* 2007). However, in climate change experiments in community ecology, the vast majority of studies have applied set increments to ambient conditions as experimental treatments in warming studies, which can be viewed as an early generation approach. This may effectively mimic effects of climate change on mean temperatures, but does not incorporate predicted changes in the frequency, intensity, and duration of extreme events.

We have concentrated here on the effects of warming, however, some of the insights we present will also apply to studies which manipulate other factors such as precipitation. Modelling for rainfall is much more difficult, but increased extreme rainfall events are projected for many regions, including south eastern Australia (Hobday & Lough 2011). Interactions between different types of climate responses (e.g. temperature and precipitation) are particularly problematic, as many climate change scenarios predict changes in the synchronicity of these events. In south eastern Australia for instance, models predict increases in the frequency of summer high rainfall events (where winter rainfall has historically been more common) and increases in extreme summer temperatures (Hobday & Lough 2011). Incorporating these interactions into climate change experiments will require the kind of down-scaling and weather scenario generation illustrated in Part three: using down-scaled climate models to generate experimental climate change treatments.

It remains a challenge to incorporate the uncertainties involved with climate model projections into experimental biological impacts research. Uncertainties in projections arise due to model processes (e.g. radiation and carbon cycle effects), differences between models (each climate group has their own model) and lack of certainty around projected emissions pathways/scenarios (Reichler & Kim 2008). These uncertainties should be taken into account by considering the distribution of possible outcomes (Semenov & Stratonovitch 2010) and ideally an experimental design that uses an ensemble of ecological treatments rather than a single realisation as demonstrated here. This is particularly important given the emerging understanding of the complexities of responses to climatic extremes and how they interact with changes in mean conditions and past history of exposure to extremes (Benedetti-Cecchi *et al.* 2006; Pincebourde *et al.* 2012).

We have illustrated here a means to use large-scale climate models to generate realistic climate change treatments for experiments. Understanding complex community and ecosystem-level responses to climate is essential (Van der Putten *et al.* 2010) and is only feasible through the use of manipulative experiments. These must be considered in a framework that includes information on evolutionary potential, spatial processes and long-term feedbacks (Dawson *et al.* 2011), but experiments are nonetheless an essential part of understanding the mechanistic basis for responses to climate. While the existing experiments have been highly informative, they have failed to incorporate meaningful patterns of climatic variability as predicted by climate models. Applying meaningful experimental treatments is a core part of this enterprise, and this review clearly shows that we need to move to a next generation of climate change experiments in community ecology.

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AUTHORSHIP

PS completed the literature review. JB developed the down-scaling procedure for generating climate change treatments, and write that section of the manuscript. RT wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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