Title

Mesocosm Experiments as a Tool for Ecological Climate-Change Research

Journal

ADVANCES IN ECOLOGICAL RESEARCH, VOL 48: GLOBAL CHANGE IN MULTISPECIES SYSTEMS, PT 3, 48

ISSN

0065-2504

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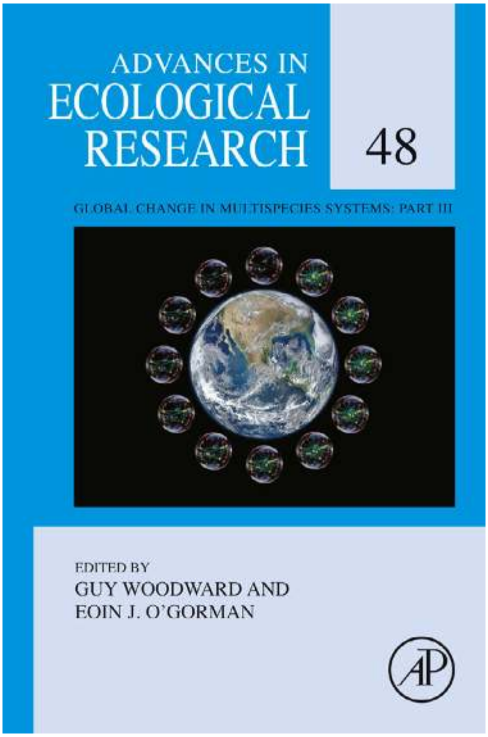
Publication Date

2013

DOI

10.1016/B978-0-12-417199-2.00002-1

Peer reviewed



From Rebecca I.A. Stewart, Matteo Dossena, David A. Bohan, Erik Jeppesen, Rebecca L. Kordas, Mark E. Ledger, Mariana Meerhoff, Brian Moss, Christian Mulder, Jonathan B. Shurin, Blake Suttle, Ross Thompson, Mark Trimmer, Guy Woodward, Mesocosm Experiments as a Tool for Ecological Climate-Change Research. In Guy Woodward and Eoin J. O'Gorman, editors: *Advances In Ecological Research, Vol. 48*,

Amsterdam, The Netherlands: Academic Press, 2013, pp. 71-181.
ISBN: 978-0-12-417199-2

Elsevier

Mesocosm Experiments as a Tool for Ecological Climate-Change Research

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Advances in Ecological Research, Volume 48
ISSN 0065-2504
http://dx.doi.org/10.1016/B978-0-12-417199-2.00002-1

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Abstract

Predicting the ecological causes and consequences of global climate change requires a variety of approaches, including the use of experiments, models, and surveys. Among experiments, mesocosms have become increasingly popular because they provide an important bridge between smaller, more tightly controlled, microcosm experiments (which can suffer from limited realism) and the greater biological complexity of natural systems (in which mechanistic relationships often cannot be identified). A new evaluation of the contribution of the mesocosm approach, its potential for future research, as well as its limitations, is timely. As part of this review, we constructed a new database of over 250 post-1990 studies that have explored different components of climate change across a range of organisational levels, scales, and habitats. Issues related to realism, reproducibility and control are assessed in marine, freshwater, and terrestrial systems. Some general patterns emerged, particularly at the ecosystem level, such as consistent and predictable effects on whole-system respiration rates. There are, however, also many seemingly idiosyncratic, contingent responses, especially at the community level, both within and among habitat types. These similarities and differences in both the drivers and responses highlight the need for caution before making generalisations. Finally, we assess future directions and prospects for new methodological advances and the need for greater international coordination and interdisciplinarity.

1. INTRODUCTION

The Earth's climate is changing rapidly and human activity is altering the planet's biota and physical properties, from local to global scales, at an accelerating rate (Rockström et al., 2009a,b; Steffen et al., 2007). Predicting the ecological consequences of climate change is not only critically important but also very difficult (Walther, 2010). This is partly because it not only includes environmental warming but also alterations to hydrology and biogeochemistry and a suite of other variables, all of which may change on average, in their extremes, and in different times and places. These components of climate change can also interact with other stressors, like eutrophication, acidification, and toxic pollution.

Causal relationships have been difficult to identify because of the reliance on inferential data. Experiments can reveal causality and the underlying mechanisms, but they are inevitably simplifications of the study systems, particularly when conducted at small spatial and temporal scales. Modelling, which could potentially improve our currently limited predictive ability, is hampered by lack of relevant ecological data and mechanistic insight (Evans, 2012). A more sophisticated approach that integrates these different methods is needed, together with larger-scale experiments that can support realistic levels of biocomplexity: mesocosms offer particular promise here (Evans, 2012; Woodward et al., 2010a).

Figure 1 Collage of various mesocosm facilities used in recent years to assess the impacts of different components of climate change on multispecies aquatic and terrestrial systems. (A) Marine mesocosms, USA (O'Connor, 2009); (B) marine mesocosms, N. Ireland; (C) marine mesocosms, USA (O'Connor et al., 2009); (D) KOSMOS marine mesocosms, Norway; (E) pond mesocosms, UK (Dossena et al., 2012); (F) pond mesocosms, Denmark (Liboriussen et al., 2005); (G) experimental flumes, Australia (Thompson et al., 2013); (H) experimental streams, UK (Ledger et al., 2013a,b); (I) tidal marsh mesocosms, USA; (J) terrestrial mesocosms, Canada; (K) Ecotron facility, France; and (L) terrestrial mesocosms, Australia (Perdomo et al., 2012). Full details and attributions are given in Appendix 1. *Photos by (A) M.I. O'Connor, (B) N. O'Connor, (C) M.I. O'Connor, (D) U. Riebesell, (E) M. Dossena, (F) E. Jeppesen, (G) R. Thompson, (H) M. Ledger, (I) J. Adrian, (J) A. Gonzalez, (K) CNRS, and (L) G. Perdomo.*

Mesocosms, which we define broadly here as experimental enclosures from 1 to several thousands of litres, are increasingly prominent in the ecological climate-change literature (see e.g. Fig. 1). The definition we apply here is unavoidably somewhat arbitrary and it includes some studies that may have previously been described as 'microcosms'; however, we apply it in a general sense for the purposes of this review, and not as a rigid, formal categorisation. One of our principal objectives is to review the current literature on mesocosm experiments, with a particular focus on those designed in line with the main climate-change scenarios outlined by the Intergovernmental Panel on Climate Change (IPCC, 2007).

1.1. Placing mesocosms in the context of ecological climate-change research

Some questions are tractable with observational studies when alternative hypotheses can be effectively eliminated by statistical techniques or modelling, but others are not, so experimentation is needed. For instance, the roles of nitrogen and phosphorus in causing eutrophication in lakes could not be distinguished without experimental tests because the two are strongly correlated in nature, and the most significant whole-system experiments were possible only after extensive meso-scale experimentation supported their central premise (Schindler, 1998).

Understanding and predicting the ecological consequences of climate change necessitates the use of multiple, complementary approaches (Fig. 2), including mesocosm experiments. Whilst smaller-scale laboratory microcosm experiments have been used frequently to relate components of climate change to physiological state or population growth rate, for example (Fig. 2: Experiment[1,2,3]), their limited realism can make extrapolations to natural systems difficult to justify. Because mesocosms can include more biological complexity at larger scales, they are generally regarded as being more amenable for testing community-level (Fig. 2: Experiment[4,5]) and ecosystem-level responses to change in more realistic settings (Fig. 2: Experiment[6,7]). They can also (ideally) help disentangle direct from indirect effects over intergenerational scales, especially for taxa that cannot be housed in microcosms, which may be especially important responses to climate change (Fig. 2: Experiment[8]).

Mathematical approaches come in many forms and include a plethora of models that can be applied to different organisational levels, from individuals to food webs to entire ecosystems (Fig. 2: Model[9,10]). For instance, mechanistic models (Fig. 2: Mechanistic models[14,15,16]) can be used to understand

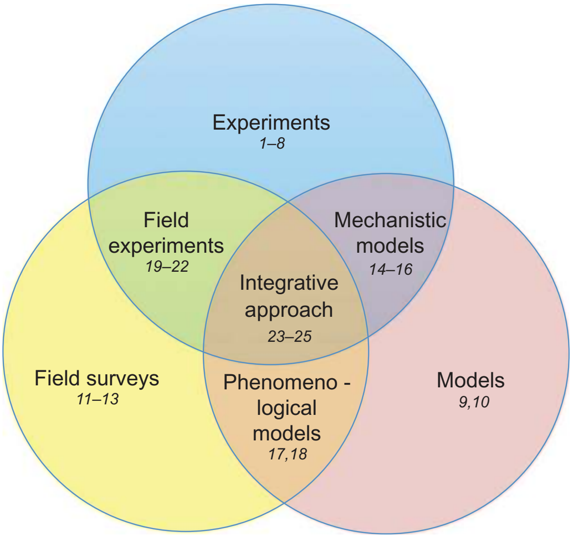

Figure 2 Classes and combinations of approaches used to investigate the ecological consequences of climate change via experiments, models, and field surveys. The intersections between classes are: mechanistic models of abiotic and biotic components based on theory and physiological knowledge; phenomenological models based on empirical observations; field experiments, including mesocosms. Reference numbers: (1) Finkel et al. (2006), (2) Vilchis et al. (2005), (3) Rall et al. (2010), (4) McKee et al. (2003), (5) Andersson et al. (2009), (6) Yvon-Durocher et al. (2010), (7) Fulweiler et al. (2007), (8) Antoninka et al. (2009), (9) Travers et al. (2009), (10) Christensen and Pauly (1992), (11) Meerhoff et al. (2012), (12) Brown et al. (2007), (13) Friberg et al. (2009), (14) Ward et al. (2012), (15) Blanchard et al. (2012), (16) Poloczanska et al. (2008), (17) Cheung et al. (2009), (18) Sheldon et al. (2011), (19) Henry and Molau (1997), (20) Perkins et al. (2012), (21) Stephen et al. (2004), (22) Meerhoff et al. (2007), (23) Friberg et al. (2009), (24) Woodward et al. (2010a), and (25) Gudmundsdottir et al. (2011a). Reference numbers are the same as in the text and Table 1.

how biotic interactions modulate ecological responses to climate change, based on first principles. Alternatively, when large volumes of data are available (Fig. 2: Phenomenological models[1,18]), other models can be used to infer future changes based on current knowledge (e.g. species distribution projections based on bioclimate envelopes). Unfortunately, many models of the ecological consequence of climate change are still inadequately parameterised, due to a lack of appropriate empirical and experimental data.

Field surveys typically explore correlations between climatic conditions and biological properties but cannot confirm causal relationships and have little or no predictive power (Fig. 2: Field surveys[11,12,13]). Field

Table 1 Examples of representative studies that used particular approaches, or their combinations, to investigate the consequences of climate change in ecological systems

	Experiments	Models	Field surveys	Mechanistic models	Phenomenological models	Field experiments	Integrated approach
(a) Effects							
Direct	*1–8*			*14–16*		*19–22*	*23–25*
Indirect	*8*			*14–16*			*23–25*
Multiple	*8*	*9,10*	*11–13*	*14–16*	*17,18*		*23–25*
							23–25
(b) Level of biocomplexity							
Individual				*14–16*			*23–25*
Population	*1,2*	*9,10*	*11–13*	*14–16*	*17,18*	*19–22*	*23–25*
Community	*3,4*	*9,10*	*11–13*	*14–16*	*17,18*	*19–22*	*23–25*
Ecosystem	*5–7*	*9,10*	*11–13*	*14–16*		*19–22*	*23–25*

Examples of research articles (italicised numbers) that addressed: (a) direct effects on organisms, indirect effects via changes in the physical environment (e.g. depth and period of water stratification), combinations of the two and (b) different levels of biological organisational complexity. Reference numbers are the same as in the text and Fig. 2.

experiments, which can bridge the gaps between such correlational data and models, include translocations, enclosure–exclosure trials, and mesocosms (Fig. 2: Field experiments[19,20]). Blending approaches, such as conducting experiments along latitudinal gradients and/or in contrasting climate regions, can combine the strengths of correlational and experimental approaches, whilst mitigating their respective weaknesses (Fig. 2: Field experiments[21,22]).

None of these approaches are perfect but in combination they can be greater than the sum of their parts, even if used primarily as a heuristic framework. They can be especially powerful when several are combined within the same model system (Fig. 2: Integrative approach[23,24,25]). For example, initial surveys by Friberg et al. (2009), Woodward et al. (2010a), Gudmundsdottir et al. (2011a), and Demars et al. (2011) on the effects of warming in Icelandic streams, were collated with new experimental data and theory in Perkins et al. (2012) and O'Gorman et al. (2012) to link structure and functioning across different organisational levels. Similarly, research assessing the replicability and realism (i.e. the ability to reproduce key properties of natural systems, such as biocomplexity) of stream mesocosms (Brown et al., 2011; Harris et al., 2007; Ledger et al., 2009) paved the way for manipulative experiments exploring drought impacts on populations, communities, food webs, and ecosystem properties (Ledger et al., 2013a,b). A third example comes from the AQUASHIFT programme developed in Germany (see Sommer et al., 2012 for a review), which contains several projects that address several components of climate change in lotic and lentic freshwaters and marine environments, as well as incorporating microcosms, mesocosms, analysis of long-term field data and modelling techniques. A deeper understanding of the ecological consequences of climate change is therefore achieved by combining multiple approaches, with mesocosms playing a central and increasingly important role.

1.2. Balancing control, replication, and realism in mesocosm experiments

Early empirical ecological climate-change research was dominated by pattern-fitting using survey data, followed by meta-analyses and experiments designed to test hypothetically important responses to climate change under more controlled conditions. There are three basic dimensions (time, space, and biological complexity) to consider, in addition to the level of replication needed to test hypotheses (Fig. 3). Because of these trade-offs, there is no one single perfect approach, and mesocosms form just one part of this jigsaw.

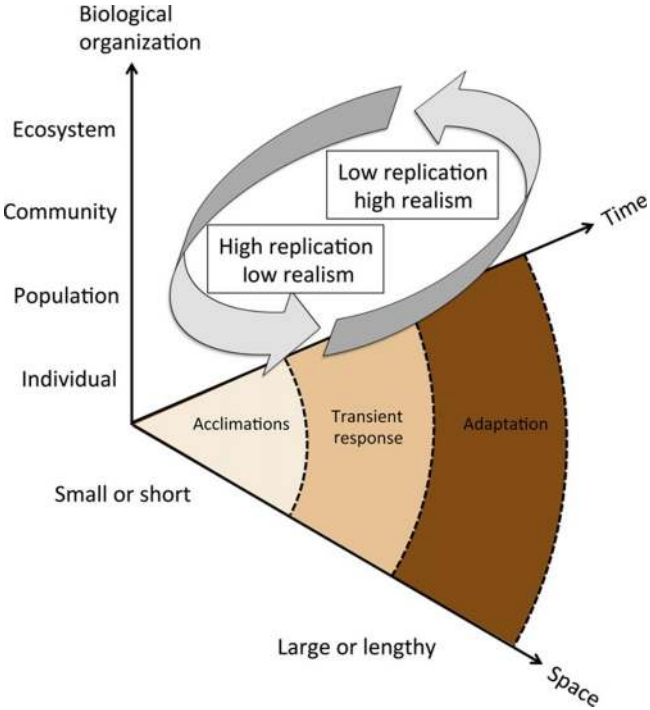

Figure 3 Conceptual diagram representing an idealised experimental domain space. Note these are arbitrary scales, not rigidly defined categories, to provide some approximate rule-of-thumb values based on the types of studies conducted to date. For instance, microscale experiments may be smaller than 1 l and run for under 1 week, whereas macroscale experiments may occupy 10^6 l and run for several decades. Here, we consider mesocosms as generally falling between these extremes. Note that spatial and temporal scales are not necessarily connected to one another or to the third dimension, organisational complexity; realism is used in the sense of the ability to reproduce key properties of natural systems.

For instance, microbial laboratory microcosms have been used to assess the dynamics of populations and simple food webs over multiple generations (e.g. Gonzalez et al., 2011; Petchey et al., 1999). Whilst protist microcosm assemblages in laboratory flasks are simpler subsets of natural communities, experiments conducted at this scale can reveal mechanisms and inform models applicable to larger, more complex systems—including mesocosms.

Ecological climate-change research is rapidly developing from correlational to more mechanistic approaches, as our understanding and ability to operate in more realistic settings improves. Much of the emerging focus is now on developing more integrated, systems-based approaches that involve mesocosms constructed at larger scales with higher biocomplexity, with the ultimate aim of parameterising, testing, and refining predictive models. Despite some common limitations, such as 'wall effects' resulting from the use of containers, that need to be borne in mind (Petersen et al., 2009) mesocosms are playing an integral role in this increasingly sophisticated and interdisciplinary field. There are financial and practical constraints on their size and the number of organisms they can house and vertebrates are often missing (except perhaps small fishes and amphibians), so only a partial picture of the full spectrum of biological responses may be achievable.

Nonetheless, they can provide invaluable information that cannot be gleaned from any of the other approaches (Bonsall and Hassell, 2005; see reviews in Benton et al., 2007; Yvon-Durocher and Allen, 2012). For example, they are essential for examining the impacts of extreme events, habitat fragmentation, or species invasions in the field, where some form of containment or (partial) isolation from the surrounding landscape is required. The merits and limitations of mesocosm experiments in general ecology have been reviewed extensively (e.g. Benton et al., 2007; Cadotte et al., 2005; Fraser and Keddy, 1997; Ledger et al., 2009), and we will not revisit these broader discussions here; rather, we will focus on their role in climate-change ecology, especially over the past two decades.

1.3. Development of the mesocosm approach in climate-change research

Mesocosms of one form or another have been used in experimental ecology since at least the early twentieth century (e.g. see review by Benton et al., 2007), but their contribution to climate-change research has only really become commonplace since about 1995 (Fig. 4). We selected this date as a (somewhat arbitrary) starting point for constructing a new database derived from 267 primary research articles (see Appendices 2–6 for methods and list of papers) as part of this chapter, to explore the major trends in research activity across different scales, organisational levels, and habitats.

The relatively slow initial uptake of the mesocosm approach in climate-change research, compared with more general ecology, reflects a combination of logistic and financial constraints and early concerns about the perceived lack of relevance when addressing global-scale issues (Carpenter, 1996). More recent work, however, has shown at least some key properties of

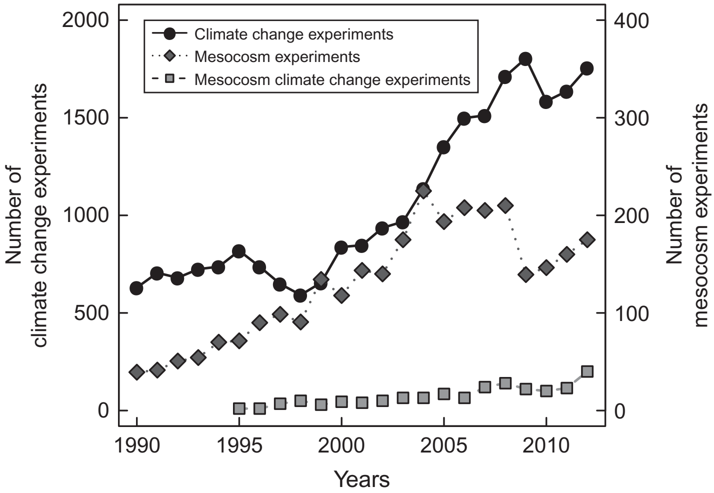

Figure 4 The use of mesocosms in ecological climate change research. Black circles represent experimental climate change studies that did not use mesocosms (data are plotted against the primary *y*-axis). Light grey squares or dark grey diamonds represent experimental mesocosm studies that either did or did not investigate climate-change impacts, respectively (data are plotted against the secondary *y*-axis). See methods (Appendix 2) for details.

global-scale survey data and model predictions are reproduced successfully in mesocosms (cf. Yvon-Durocher and Allen, 2012; Yvon-Durocher et al., 2010a,b, 2011a,b, 2012), allaying these concerns to some extent and demonstrating how careful testing of process-based hypotheses can advance climate-change science. More resources are now being diverted into larger-scale, longer-term mesocosm studies, as the need for more realistic testing of theories and models in the field is being recognised. The recent surge in mesocosm-based papers (Fig. 4), as well as substantial new infrastructure investment in highly instrumented sets of chambers, for example, the Ecotrons, designed for ecosystem research under controlled environmental conditions (De Boeck et al., 2011; Lawton, 1996), reflect the increasing prominence of large-scale experimentation. Ideally, mesocosm experiments should be embedded strategically within a larger empirical and theoretical framework as part of more ambitious, integrated, and interdisciplinary studies. In reality, we are often still forced to extrapolate from isolated, uncoordinated, and contingent case studies and to rely on meta-analysis, rather than generating the new data that are really needed, points we will return to in the latter part of this chapter.

We subdivided our database to explore how research effort has been apportioned across different ecosystem types (marine, freshwater [lentic and lotic waters], terrestrial), spatial and temporal scales, and organisational levels, as well as among the different components of climate change. We defined mesocosms as being either small ($<10^2$ l), medium (10^2–10^4 l), or large ($>10^4$ l) and the absolute duration of the experiment was defined as short (<1 month), medium (1 month–1 year), or long (>1 year). The relative duration (based on the typical lifespan of the focal organism group in each study) was defined as short (<1 day), medium (1–100 days), or long (>100 days). The level of biological complexity investigated was defined as population, community, or ecosystem. To avoid double counting, studies that investigated multiple level of biological organization were counted only once and were assigned to the highest level. These distinctions are necessarily somewhat arbitrary, as were the search terms used to locate and include/exclude potential papers; as such, this is neither a precise nor an exhaustive list, rather it represents a broad overview using a standardised set of criteria (see Appendices 2–4 for further details about the database). Papers were then classified according to the highest level of biological organization: thus, if a paper published population data for a single species and also data on the entire community, it was defined as a community level study.

Rather than conducting a full, formal meta-analysis on these data, here we simply explored some of the major statistical patterns, using contingency tables to test for associations among classes defined by different combinations of grouping factors (i.e. components of climate change, ecosystem types, levels of biological complexity, temporal and spatial scales), as depicted in Figs. 5–7. Permutation tests for conditional independence were performed and residual-based shading (Figs. 6, A1 and A2) was used to identify departures of M statistics from independence among classes (i.e. the observed frequencies are significantly higher or lower than the expected frequencies; Zeileis et al., 2007; see Appendix 4 for details of the analysis).

Overall, warming and increased atmospheric CO_2 concentration were by far the most intensively investigated components (Figs. 5A and 6A; $M=7.404$, $P<0.001$). In relation to increasing atmospheric CO_2 levels in terrestrial systems, huge emphasis has been given to ‘fertilisation’ effects in photosynthesis, whereas in marine systems CO_2 change has been investigated primarily in the context of ocean acidification, and in freshwaters it has been largely ignored. Perhaps unsurprisingly, the consequences of floods and droughts have been examined mostly in the terrestrial literature (but see, Ledger et al., 2013a,b for a freshwater exception), reflecting the

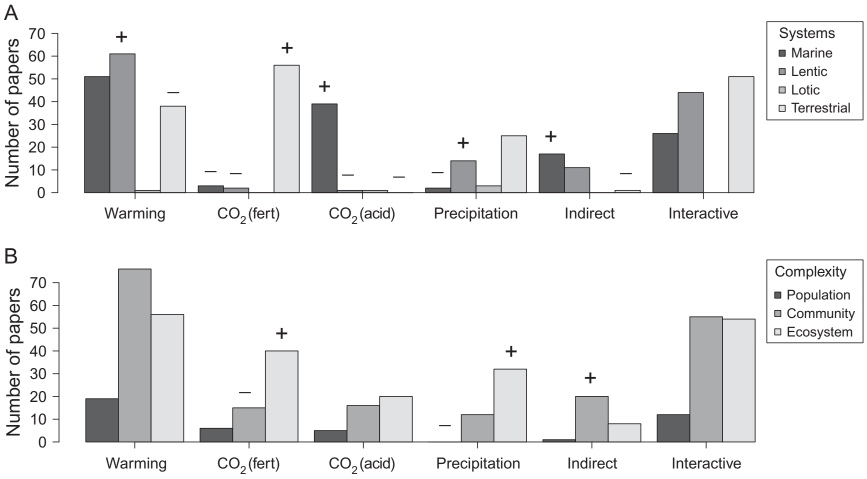

Figure 5 Number of mesocosm studies investigating climate-change impacts in different habitats (A) and levels of biological organisation (B). Direct components of climate change include: warming, CO_2 fertilisation, CO_2 acidification, and changes in precipitation. Indirect components include simulated changes in UV radiation, surface water run-off, salinity, and sea level. Interactive refers to those studies that address synergies with other anthropogenic stressors (e.g. nutrient enrichment, pollution, habitat alteration). +/− indicate classes where observed frequencies were significantly higher or lower than the expected frequencies (see Appendices 2–5 for further details: note total counts can exceed the number of studies if multiple components were manipulated simultaneously).

pressing concerns about future water security and the potentially huge socio-economic costs of such extreme events, especially in agricultural or urban landscapes.

Figure 5 highlights how many of the more subtle, indirect effects, and synergies between components of climate change have been largely ignored in terrestrial systems, yet have been considered more widely in aquatic systems (e.g. changes in cross-ecosystem subsidies due to altered precipitation patterns). A few recent studies have also investigated the interactions between climate change and other stressors, such as habitat fragmentation (Perdomo et al., 2012), changes in diversity, and nutrient regimes (Moss, 2010).

It has to be noted that we classified studies accordingly to the highest level of biological organisation investigated. Therefore, the frequency of population-level studies might be underestimated as population-level metrics are often reported within the context of community-level studies.

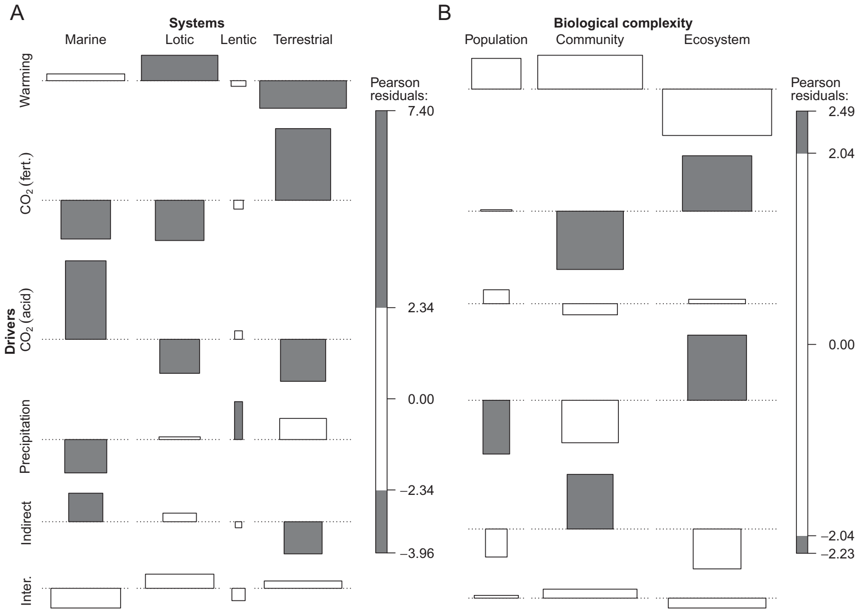

Figure 6 Statistical association plots derived from the data used in Fig. 5A and B. Rectangles represent the classes of two-way contingency tables constructed using the following grouping factors: (A) habitat type and components of climate change and (B) level of biological complexity and components of climate change. Reference bars represent the distribution of the simulated *M* statistics and the respective positive and negative cut-off values at critical $\alpha = 0.1$. Cells in which the critical *M* value was exceeded (i.e. the observed frequencies are higher/lower than those expected) are shaded in grey; positive and negative *M* values are represented as departure above or below the dashed reference line, respectively. The width of the cells is proportional to the sample size.

Very few long-term, large-scale experiments have been conducted (Figs. 7A and A1A; $M = 2.667$, $P = 0.012$), reflecting the huge resource costs involved, despite these being the scales of most direct relevance to ecological climate-change research. Large experiments are crucial because extrapolation from smaller scales can be unreliable, and long-term experiments are needed to fully understand the dynamic response of ecosystems to climate change beyond the transient effects of short-term perturbations. There is a danger that many mesocosm studies might display a 'random-walk' from the initial conditions, which if stopped too early, could be misinterpreted in terms of weak or idiosyncratic treatment effects but which may become more pronounced and consistent over time (Chave, 2013). A major obstacle to resolving this lies in convincing funding bodies to

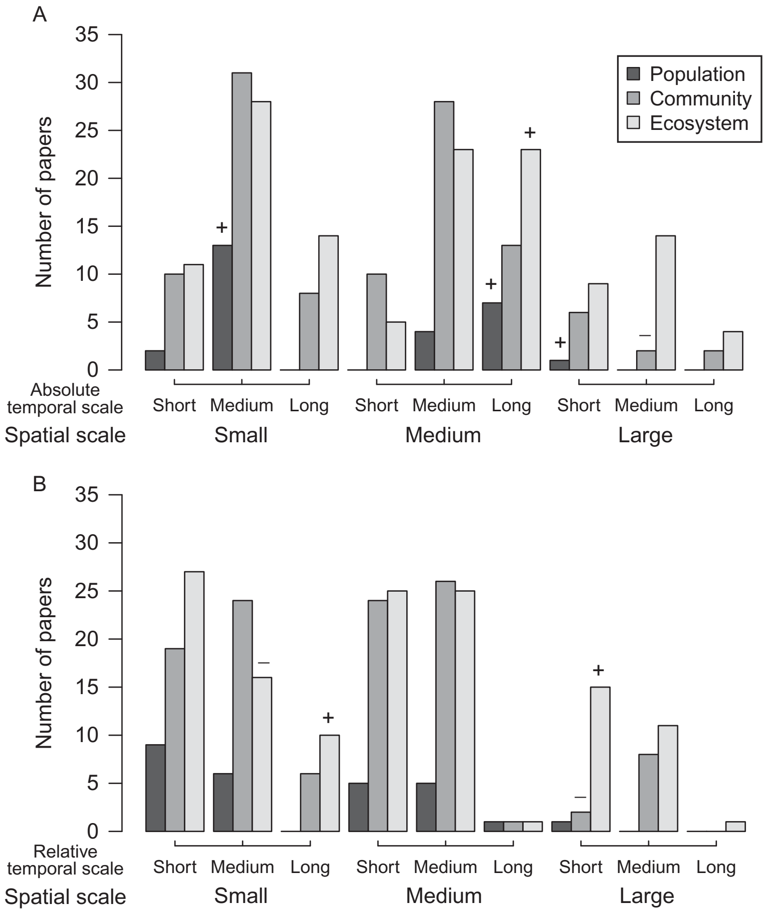

Figure 7 Number of mesocosm studies of different scales and organisational levels used to investigate the effects of climate change. In (A), the timescale is expressed in absolute terms, whereas in (B), it is shown as a fraction of the lifespan of the focal taxa (see Appendix 3 for details). Spatial scale is arbitrarily defined as small (<100 l), medium (100–10000 l), or large (>10000 l).

support long-running experiments that would allow intergenerational effects to filter through the morass of pathways in the food web, an issue we return to in Section 4.

One way to view these effects in a more standardised manner may be to define experimental duration not as absolute units of time, but relative to the lifespan of the focal or longest-lived taxon in multispecies studies (Yodzis, 1988). Such definitions are inevitably somewhat subjective. Here, we define the *focal taxon* as the main taxonomical group investigated in the study, or, when conducted in multispecies systems, the longest-lived organism(s) mentioned explicitly in the paper; then we assigned the *focal taxa* to broad categories based on their approximate lifespan (e.g. the majority of fish live for >1 year; see Appendix 3 for details). As we rescaled our data from calendar time to lifespan units, the number of long-term experiments generally declined and the number of short- and medium-term increased, except for those at small spatial scales, where the number of long-term experiments increased (Figs. 6B and A1B; $M=2.335$, $P=0.041$). This was because medium and large mesocosms generally included large, long-lived organisms (e.g. fishes), whilst small mesocosms contained smaller organisms with much shorter lifespans (e.g. protists). Overall, our analysis reveals some marked biases in the data that hampers our current ability to generalise about the likely effects of climate change in different systems. This is further complicated by the possibility that some studies may be more prone to transient dynamics in response to (potentially unrealistically) rapid change (e.g. short absolute time but with long-lived organisms), whereas others may be closer to equilibrial conditions that could arise due to longer exposure to the stressor of choice (e.g. long absolute time but with microbial biota as the focal organisms).

Marked differences were evident in how climate-change mesocosm approaches are applied in freshwater, marine, terrestrial, and wetland systems, in terms of not only the component under investigation (Fig. 5A) but also the scale of the study (Fig. 8A and B). Freshwater (lentic and lotic) experiments were generally of intermediate length and size, whereas marine and terrestrial experiments are more evenly distributed across scales (Figs. 8A and A2A; $M=2.638$, $P=0.012$). When the temporal scale was expressed in lifespan units (Fig. 7B), there was an increase in the number of long-term terrestrial and marine experiments (Fig. A2B; $M=2.411$, $P=0.048$) focused on short-lived seasonal grasses and marine plankton, respectively.

The disparities across ecosystems may reflect differences in the ease with which experiments may be carried out, but this will inevitably introduce methodological biases in the literature that must be kept in mind when drawing general inferences (or conducting more formal extensive meta-analyses).

2. MESOCOSM APPROACHES IN DIFFERENT HABITATS

In this section, we gauge how mesocosms have been used in different aquatic and terrestrial habitats to examine the effects of the main components of climate change in multispecies systems, with a focus on drought, warming,

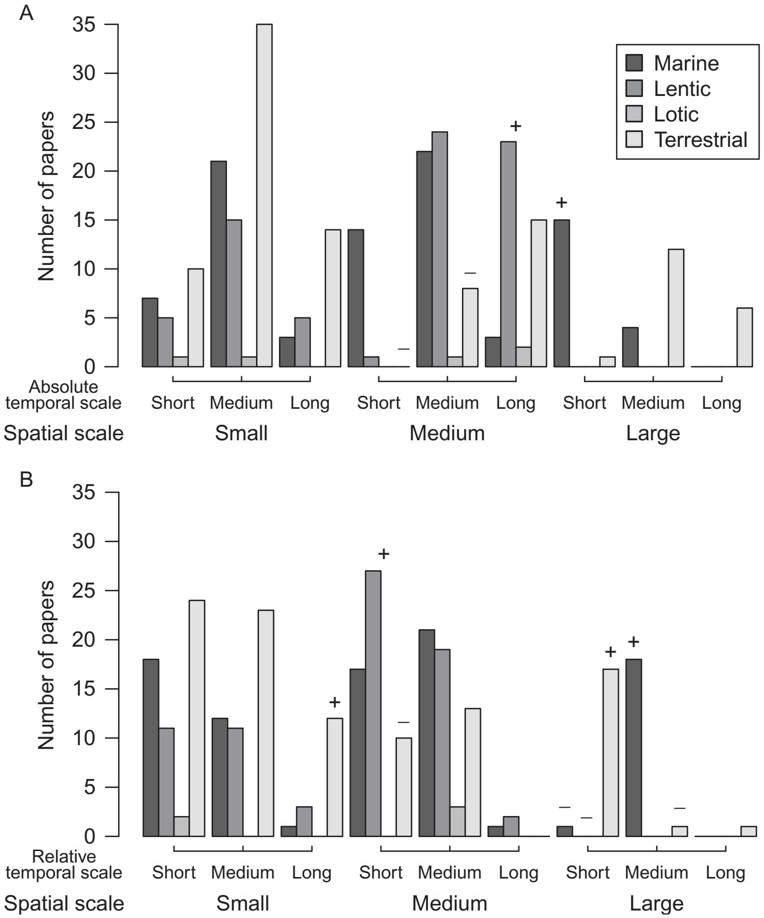

Figure 8 Number of mesocosm studies conducted at different scales to investigate the effects of climate change in different ecosystems. In (A), the timescale is in absolute terms, whereas in (B), it is shown as a fraction of the lifespan of the focal organisms used in the experiments (see Appendix 3 for details). Details are otherwise the same as in Figs. 5 and 7.

and CO_2 enrichment. The text for each habitat follows a general structure of addressing the historical background of climate-change mesocosm research relative to other approaches, the main results to date and evidence of any consistent patterns, followed by a consideration of caveats and future directions specific to that habitat (a more general overview and assessment of future directions is provided later). This exercise also explores the extent to which each habitat has been investigated in isolation or whether cross-system linkages have been considered (e.g. terrestrial leaf-litter fuels many stream food webs; Hladyz et al., 2009, 2011). We have defined three broad divisions here: (1) marine, coastal, and estuarine systems; (2) freshwaters (lentic and lotic systems); and (3) terrestrial systems. These broad categories can of course be subdivided or aggregated further, and some transitional habitats span several categories, but they offer a useful oversight of broadly differing systems, whilst retaining reasonable sample sizes. Wetland habitats were poorly represented overall and therefore were assigned to either the marine or freshwater categories, depending on whether they were predominantly saline or brackish (e.g. brackish marshes and mangroves accounted for 2% of marine systems) or not (e.g. bogs, fens, reedbeds accounted for 19% of lentic freshwaters). Running waters, although also poorly represented, were given their own subdivision within freshwaters because they are fundamentally different from standing freshwaters and other systems in many ways (e.g. unidirectional flow and distinct assemblages of rheophilic taxa).

2.1. Marine, coastal, and estuarine ecosystems

Conducting experiments in marine systems presents a variety of challenges: the subtidal zone in particular is one of the most difficult (and expensive) environments in which to work and most studies have been necessarily observational, requiring highly specialised equipment and personnel. Working in the intertidal environment is easier but restricted to the interval between high tides. Manipulative experiments are possible but require hardy construction due to eroding salt water and powerful wave forces (Denny and Gaylord, 2002). Transitional brackish waters may be more accessible, but these pose their own problems, not least due to changes in inundation and salinity with the rise and fall of the tide. Aquaria and mesocosm experiments, on the other hand, have little in the way of time or weather constraints, and materials are relatively cheap and easily accessible, although it can be extremely difficult to mimic natural conditions. In the 1970s, mesocosm use became popular in marine research (Hodson et al., 1977) and they are now commonplace, with increasingly complex experimental and technical designs (O'Gorman and Emmerson, 2010; Twomey et al., 2012).

Climate change factors have been examined in marine systems since at least the early twentieth century, although only recently in the context of anthropogenic change (e.g. Jacob et al., 2011; Möllmann and Diekmann, 2012; Peck et al., 2012; Rossberg, 2012). Pelagic marine environments are relatively homogeneous compared with terrestrial environments, although changes in currents, tides, and terrigenous run-off cause variation in salinity, temperature, and dissolved nutrients and coastal intertidal habitats experience extreme fluctuations in physical conditions. Precipitation and salinity have long been considered important structuring forces in these habitats (Beadle, 1931; Braarud, 1951; Goodbody, 1961), but the realisation that climate change will alter patterns of precipitation has renewed interest in their influence (Struyf et al., 2004).

The importance of temperature and CO_2 in marine systems have long been recognised (Smith and Roth, 1979) and these now form the focus of modern marine climate-change research (Fig. 5A; Wernberg et al., 2012). Ocean acidification arises when excess atmospheric CO_2 reacts with seawater to increase concentrations of hydrogen ions and reduce carbonate ions (which are key building blocks for calcified shells and skeletons). Hydrogen ion concentrations of the surface ocean have already increased by 30% in just 15 years (SCOR, 2009) and may increase by as much as 150% by the end of the century (IPCC, 2007). Climate change is also expected to affect upwelling, nutrient delivery, storminess, coastal salinity, and sea level rise, which is predicted to increase 0.18–0.56 m by 2100 (IPCC, 2007). Intertidal coastal ecosystems are at particular risk from rising sea level, extreme heat events, increased storm occurrence, and flooding due to climate change (Harley, 2011; Harley et al., 2006), with many predicted to undergo dramatic transformations into very different habitats (e.g. salt marsh replaced by fen). Some of these aspects of climate change and its synergies with other stressors may be reproducible in mesocosms (e.g. warming × eutrophication), whereas others are not (e.g. storminess × overfishing).

Warming and ocean acidification are two of the most serious threats to marine systems and have been investigated via ‘natural experiments’ across environmental gradients (Hall-Spencer et al., 2008; Kroeker et al., 2011; Schiel et al., 2004). Such areas are usually quite rare, often precluding proper replication of treatments and may be isolated patches of atypical conditions, so the resulting community is not necessarily representative of changing conditions because the regional species pool is depauperate (Schiel et al., 2004). Space-for-time substitutions have been used at different spatial scales (e.g. Leonard, 2000; Morelissen and Harley, 2007; Petes et al., 2008), but often the abiotic variable of interest (e.g. temperature) is not the only factor that varies with location. Warming experiments on marine planktonic communities have been conducted, for example, O’Connor et al. (2009) described how the effect of warming on food web structure can be modulated by both the type of control on dynamics (top-down vs. bottom-up) and the availability of resources (Fig. 9A–D).

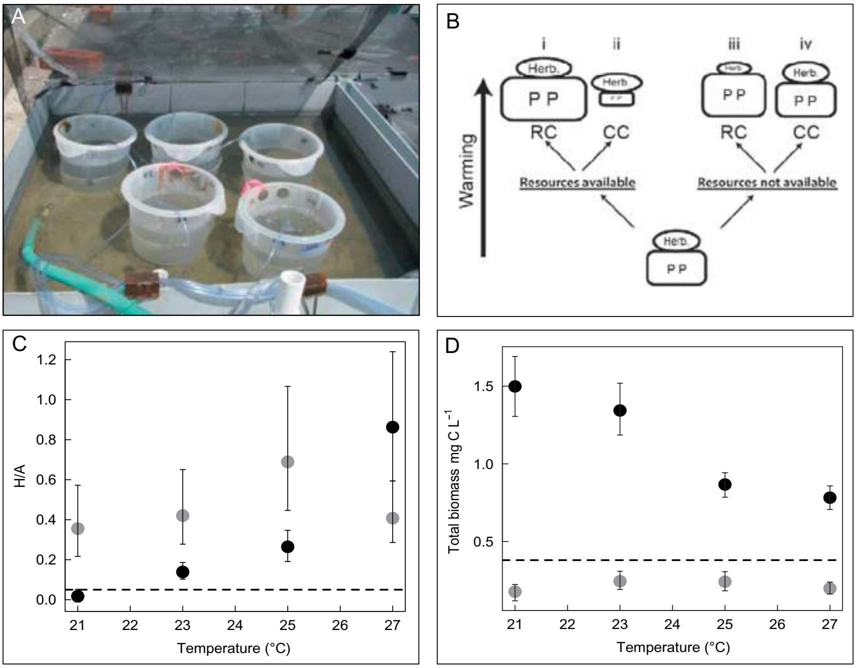

Figure 9 (A) Marine mesocosms used to investigate interactive effects of warming and nutrients on consumer-controlled (CC) or resource-controlled (RC) food webs. (B) Resource availability constraints on primary production (PP), whilst metabolic constraints influence both primary producers and herbivores (Herb.). The metabolic effects of temperature are orthogonal to those imposed by resource availability. (C) Effect of temperature on the ratio of heterotroph to autotroph (H/A) biomass, and (D) the carbon biomass of the entire food web in the presence (black circles) and absence (grey circles) of nutrient enrichment. Dashed lines represent initial conditions. *Redrawn after O'Connor et al. (2009).*

Field manipulations of temperature and CO_2 are rare, due to the difficulty of containing warmed or acidified water (Barry, 2005; but see, Campbell and Fourqurean, 2011). Studies of community responses to aerial thermal stress in the intertidal have traditionally used cooling (by shading) rather than warming treatments (Kon et al., 2010; Morelissen and Harley, 2007; Williams, 1994) but, because intertidal species often live near their thermal maximum, 3 °C of cooling cannot necessarily predict the effects of 3 °C of warming. Recently, warmed settlement plates that allow for natural community development in the field have been created to heat the substratum in the intertidal (Kordas et al., in review) and a small boundary layer of water in the subtidal (Smale and Wernberg, 2012). These methods allow for high replication, they can be used over large distances (though the unit is small) and are inexpensive.

There is a long history of using natural (Dethier, 1984; Paine and Vadas, 1969) or artificial *in situ* rock pools as ‘pseudo’ mesocosms (Castenholz, 1961; Polte et al., 2005; Romanuk et al., 2009) to manipulate communities, but not (yet) in the context of climate change. Due to problems associated with water mixing, many marine climate-change experiments have been conducted in smaller (1–100 l) indoor/laboratory mesocosms, with artificial light and fine temperature control (e.g. Fig. 1A). Artificial seawater can even be created in the laboratory (e.g. Instant Ocean®) and run through a filtration system, if high levels of control of its chemical composition are needed. These experiments typically involve small-to-medium individuals (esp. larval life stages), small populations, and one or two interacting species. Larger (100–10,000 l) and more realistic mesocosms are usually located outdoors and tend to be exposed to ambient light and temperature, whilst using nearby ‘flow-through’ seawater (e.g. Fig. 1D). Mesocosms (indoor or outdoor) that mimic tidal regimes are feasible in some designs, but these are still rare (Stachowicz et al., 2008).

Experiments examining ocean acidification have attempted to discern the physiological and ecological responses to pH of particular processes, such as respiration (Wood et al., 2008), calcification (Gazeau et al., 2007), and fertilisation (Byrne et al., 2009). Meta-analyses have found that marine biota vary widely in their sensitivity to acidification (Kroeker et al., 2010, 2013): in general, calcifying organisms (e.g. corals) are more negatively affected by increased $p\mathrm{CO}_2$ than non-calcifying organisms. Increased $p\mathrm{CO}_2$ can, however, actually enhance growth in fleshy algae and diatoms (Kroeker et al., 2013). In addition, there is considerably more variation in species responses to acidification when tested in multispecies systems (Kroeker et al., 2013) suggesting that interspecific interactions reduce predictability at the community level (Hale et al., 2011). However, it is difficult to generalise, as fewer than 40 studies have examined biological responses to ocean acidification in multispecies systems, emphasising an important gap in our knowledge.

In 2001, a large interdisciplinary group of European researchers formed the Pelagic Ecosystem CO_2 Enrichment (PeECE) Study to examine the effects of ocean acidification on marine plankton communities using nine large (11,000 l) polyethylene mesocosms, moored nearshore in Norway (Engel et al., 2005). $p\mathrm{CO}_2$ concentrations corresponding to glacial, present, and projected levels were established in triplicate by bubbling CO_2/air mixes into seawater. The mesocosms were filled with local seawater and a phytoplankton bloom was initiated by adding nutrients. Biogeochemistry, plankton physiology and population dynamics, and community structure were measured over 19 days. In 2003 and 2005, similar experiment was run using even larger (20,000 l) mesocosms. Although a plankton bloom was successfully created in all three experiments, the responses of the ecosystem to CO_2 enrichment were complicated. For example, there was no effect on the abundance and diversity of bacteria, micro-zooplankton grazing, copepod feeding, and reproduction, whereas bacterial production, viral abundance and diversity, and copepod recruitment were affected (summarised in Riebesell et al., 2008).

Since then, several more ambitious mesocosm experiments have been implemented under the umbrella of MESOAQUA, including the Kiel Off-Shore Mesocosms for future Ocean Simulations (KOSMOS) project, which deployed its first off-shore experiment in 2010, near Svalbard, Norway (Fig. 1D). The structure of the mesocosms was similar to the PeECE design, but they were much larger (50,000–75,000 l), more robust to off-shore conditions, and non-destructively encapsulated a column of water by closing a bag around it (instead of using a pump, which can damage fragile plankton). The arenas incorporated wall scrubbers, to address one of the common criticisms levelled at mesocosm experiments, and ran for many weeks (Riebesell et al., 2012). The improved methods allowed for more realistic abiotic and biotic conditions and reduced some common artefacts of mesocosms (e.g. wall effects). Preliminary results reveal that high CO_2 reduced production rates and pushed the system towards more retentive food webs, that is, those that recycle organic matter and minimise losses due to sinking (Czerny et al., 2012).

We need to improve our understanding of the effects of ocean acidification and warming on marine organisms in general, and on keystone species in particular, at different stages of the life cycle and at the ecosystem level of impacts. These impacts must also be placed within the wider context of other stressors, and mesocosms provide an important means with which to do this. Mimicking climate-change conditions *ex situ* nevertheless presents challenges. The first ocean acidification experiments simply added acids and bases to manipulate the pH of seawater, but this was abandoned when researchers discovered that it was not only reduced pH that affected organisms but also changes in the carbonate chemistry. Since then ‘standard operating procedures’ have been developed (Dickson et al., 2007), which include using bubbled CO_2 to create treatments and recommendations for the careful monitoring and control of water chemistry. This requires careful monitoring and is prone to mishaps, so long-term (>5 months) experiments are rare (Kroeker et al., 2013), precluding experiments that span entire life histories or at evolutionary scales, except for the shortest-lived organisms.

As methods become increasingly standardised and with a growing technological capability and expertise, the number of experiments has increased exponentially, with over 200 papers published on ocean acidification from 2010 to 2012 alone (Kroeker et al., 2013). Acidification experiments are now far more common than warming experiments (Wernberg et al., 2012), and mesocosm approaches are becoming more widely used (Harley et al., 2006; Hawkins et al., 2008; Wootton et al., 2008). The focus on acidification undoubtedly reflects the publication of high profile reports, such as the European Project on Ocean Acidification, EPOCA (Gattuso and Hansson, 2009).

Long-term changes in the frequency, intensity, timing, and distribution of extreme events in marine and coastal environments (e.g. hurricanes and tropical storms) will have impacts on multiple species and their interactions, as well as underlying processes, such as nutrient cycling and primary and secondary productivity. Very few studies that span multiple generations of the focal taxa have been attempted (except for bacteria and protists in laboratory microcosms), so there is currently a severe lack of information about the potential for individuals, populations, and communities to adapt to ocean acidification in the longer term (Figs. 5–8). Future studies need to address this gap in our knowledge by employing long-term experiments, field monitoring programmes, and ecological modelling to increase our currently very limited predictive power.

2.2. Freshwater mesocosms in lentic and lotic ecosystems

Recent experimental work in lentic ecosystems has been motivated by the increasingly intense impacts of human pressures and by the need to inform policies to mitigate their negative effects on fresh waters. Observational studies, although widely used, often cannot disentangle different drivers, which is where the direct evidence of controlled experiments is especially valuable. Small-bottle incubations, *in situ* mesocosms, and whole-lake experiments have all been conducted since the early 1970s in the Experimental Lakes Area, Canada, to investigate eutrophication and acidification (Schindler, 1998) and since then, the use of mesocosms has proliferated, despite debate on their value relative to other experimental approaches, particularly whole-ecosystem experiments (Schindler, 1998 and references therein; Spivak et al., 2011). Thus, although the focus on climate change is much more recent, many of the practicalities and advantages and disadvantages of the approach are already familiar to limnologists, and many variations on the mesocosm theme have been used in different contexts. These include small (plastic) enclosures containing plankton systems open to the atmosphere (e.g. Lacerot et al., 2013); larger enclosures of flexible or rigid polyethylene open to the sediments and atmosphere (Beklioğlu and Moss, 1995); and ponds, either created by dams (Balls et al., 1989) or established in tanks on land (Liboriussen et al., 2005; McKee et al., 2000, 2002a,b; Yvon-Durocher et al., 2011a,b). The relative importance of top-down and bottom-up forces in shallow lakes has been widely investigated using mesocosms under different environmental conditions, including environmental warming (e.g. McQueen et al., 1986; Williams and Moss, 2003; Williams et al., 2002). More recently, an ambitious programme that spanned a latitudinal gradient in Europe combined space-for-time surveys with mesocosm approaches (Bécares et al., 2008; Gyllström et al., 2005; Moss et al., 2004; Romo et al., 2004; Stephen et al., 2004).

Several mesocosm experiments have explored the effects of climate change in freshwater systems since the first studies in the late 1990s (e.g. Beisner et al., 1997), and most of these have since then largely focused on temperature (mostly on increases but also its variation) in lentic systems. The heating systems used have varied from open-top chambers (e.g. Netten et al., 2010; Strecker et al., 2004) using transparent covers to create a local greenhouse effect, to the installation of electrical elements or hot water pipes inside the mesocosms. The latter include a range of pond mesocosms, which represent the most ambitious systems used so far, such as the broadly similar set ups in the United Kingdom (Liverpool: Feuchtmayr et al., 2010; McKee et al., 2003; Moran et al., 2010; Moss et al., 2003 and Dorset: Yvon-Durocher et al., 2010a,b, 2011a,b), Denmark (Jeppesen et al., 2010a,b; Liboriussen et al., 2005, 2011), and Canada (e.g. Greig et al., 2012; Kratina et al., 2012). Several of these experiments have analysed the interactive effects of nutrient enrichment and predation pressure with warming.

Very few studies have addressed other aspects of climate, such as UV radiation (Williamson et al., 2010), CO_2 enrichment (Andersen et al., 2005), precipitation or water level changes (Bucak et al., 2012; Berger et al., 2007, 2010), and acidification (Christensen et al., 2006), in either isolation or interacting with some of the more obvious aspects (e.g. Christensen et al., 2006; Williamson et al., 2010). Some have studied indirect consequences of climate change, such as increases in run-off (Graham and Vinebrooke, 2009), salinisation (Herbst and Blinn, 1998; Jeppesen et al., 2007), and browning by increasing concentrations of humic substances in the water column (Mormul et al., 2012; Nicolle et al., 2012). Some of the ultimate consequences of climate change, such as cycling of nitrogen (Veraart et al., 2011) and carbon (Atwood et al., 2013; Flanagan and McCauley, 2010; Liboriussen et al., 2011; Moss, 2010; Yvon-Durocher et al., 2010a,b, 2011a,b), benthic–pelagic or terrestrial–aquatic coupling (Boros et al., 2011; Greig et al., 2012), or the implications of biodiversity change for ecosystem stability (Thompson and Shurin, 2011) have only recently been addressed using pond mesocosms.

Most mesocosm studies have focused on climate effects on plankton (particularly phytoplankton) dynamics and addressed processes at the community level (e.g. Feuchtmayr et al., 2010; McKee et al., 2002a; Moss et al., 2003; Nicolle et al., 2012; Strecker et al., 2004). Fewer have considered other groups, such as microbes (Christoffersen et al., 2006; Özen et al., 2012; Shurin et al., 2012), macrophytes (Feuchtmayr et al., 2009; Netten et al., 2010; McKee et al., 2002b), macroinvertebrates (Baulch et al., 2005; Dossena et al., 2012; Feuchtmayr et al., 2007; Greig et al., 2012), or fish (Moran et al., 2010). When fish are included (either as a predation treatment, e.g. Liboriussen et al., 2005; McKee et al., 2002a,b, or as a response variable, e.g. Moran et al., 2010), a single, small species has been used, highlighting the limitations of mesocosms in accommodating the several species and large size ranges found in natural lakes. Other organismal responses to global drivers, such as evolutionary adaptation of zooplankton species (Van Doorslaer et al., 2007, 2009), or changes in the chemical composition of organisms with warming (Ventura et al., 2008) are also currently underrepresented areas in lentic mesocosm research.

The conclusions of mesocosm experiments in standing waters have sometimes differed from those of other approaches, such as long-term surveys (e.g. Adrian et al., 1999), space-for-time substitutions (e.g. Meerhoff et al., 2012), or paleolimnogical studies (e.g. Battarbee et al., 2005). For instance, the body size of aquatic ectotherms has been suggested to decrease with warming (Daufresne et al., 2009; but see, Gardner et al., 2011). In heated freshwater mesocosms, the evidence is sometimes contradictory: in one study (Fig. 10A), warming shifted the structure of phytoplankton (but not the zooplankton) assemblages in favour of smaller species (Fig. 10B; Yvon-Durocher et al., 2011a) and benthic macroinvertebrates (Fig. 10B; Dossena et al., 2012). Other experiments found no effect on size (Moss et al., 2003). Space-for-time substitution studies have

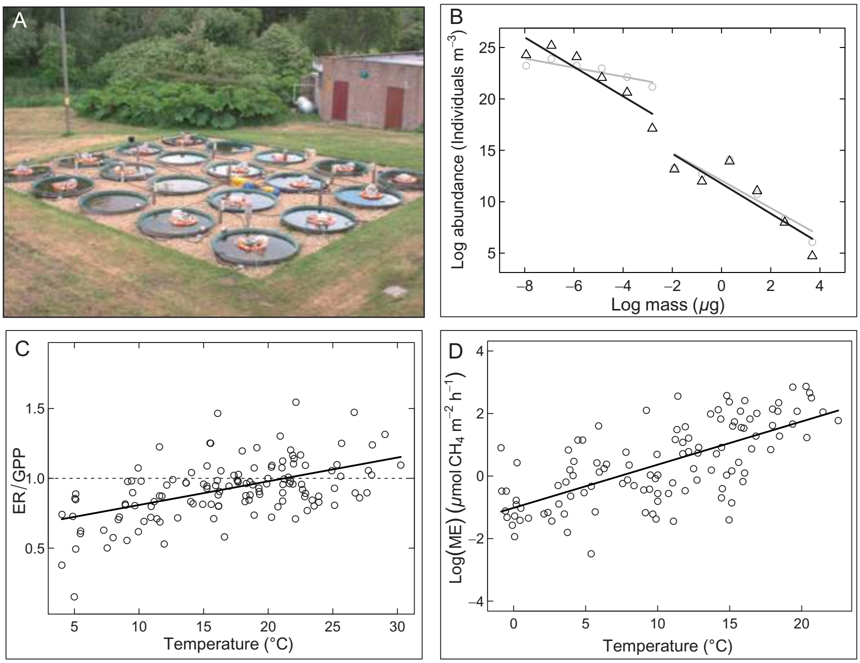

Figure 10 Mesocosm experiments in shallow freshwater ecosystems showed that warming has the potential to simultaneously alter community structure and ecosystem functioning. (A) Experimental setting. (B) Pelagic and benthic size-spectra slopes were steeper in warmed (black triangles) versus ambient communities (grey circles), due to increased abundance of small autotrophs. (C) Changes in community structure were accompanied by changes in the balance between ecosystem respiration (ER) and gross primary production (GPP); warmed systems exhibited greater heterotrophy (ER/GPP > 1) and (D) an increase in whole ecosystem methane efflux. *Redrawn from Yvon-Durocher et al. (2010a,b, 2011a,b) and Dossena et al. (2012). Photo: M. Dossena.*

found body size declines with decreasing latitude (i.e. warmer conditions) for lake fish and cladoceran zooplankton (Gillooly and Dodson, 2000; Jeppesen et al., 2010b, 2011), although comparable data are still lacking for many other groups (Meerhoff et al., 2012).

Other mesocosm studies suggest that warming may have very minor effects on phytoplankton Chl-a and total biovolume with a 3 °C rise in a 2-year mesocosm experiment, although stronger effects were evident with 4 °C warming (but not on cyanobacteria abundance; Feuchtmayr et al., 2009; Moss et al., 2003), whereas in other cases warming may reduce the occurrence of algal blooms under eutrophic conditions, through increased effects of zooplankton grazing, as well as fish predation on zooplankton (Kratina et al., 2012; Shurin et al., 2012). By contrast, after 2 years of experimental heating, the Danish mesocosms (Fig. 1F) revealed that warming increased phytoplankton Chl-a markedly at low nutrient concentrations under the IPCC A2 and A2-plus50% scenarios, and at high nutrient concentration in the former but not in the latter scenario, where filamentous algae became dominant (Jeppesen et al., 2010a). Allelopathic effects of these filamentous algae on phytoplankton might explain the low phytoplankton biomass in these mesocosms (Trochine et al., 2011). A higher phytoplankton biomass (especially cyanobacteria) under warm climates is in line with suggestions of space-for-time studies (Jeppesen et al., 2010a; Kosten et al., 2012; Meerhoff et al., 2012), long-term data (Jeppesen et al., 2003; Kernan et al., 2010), and reviews (Moss et al., 2011) that eutrophication and warming amplify each other's effects. However, recent laboratory competition experiments found that cyanobacteria and green algae grow equally well under experimental warming, suggesting that competitive advantages are linked to other characteristics besides growth rate (Lürling et al., 2012).

Despite these broad generalities, species-specific effects at the community level can appear to be idiosyncratic and hard to predict. For instance, of 90 phytoplankton species investigated in one mesocosm warming experiment, two species increased in abundance, two declined, and the rest were unaffected (Moss et al., 2003). Some of this variation might be due to biotic interactions modulating the effects of warming, which may be hard to resolve in multispecies systems (Reuman et al., 2013). Community responses to warming may depend on food-chain length or the trophic position of the focal taxa: Hansson et al. (2012) found that phytoplankton benefit in three-, but not in two-trophic-level systems in a mesocosm experiment, whereas cyanobacteria benefitted from a higher temperature and humic content irrespective of food-chain length.

The effects of experimental warming on zooplankton have also been highly variable. In warmed alpine mesocosms, zooplankton biomass was suppressed due to a decline in large cladocerans, even in the absence of fish (Strecker et al., 2004). However, no clear effects on the densities of zooplankton (McKee et al., 2002a) and macroinvertebrates (Feuchtmayr et al., 2007; McKee et al., 2003) were detected in mesocosms in the United Kingdom or Denmark (Özen et al., 2012). Both phytoplankton and zooplankton advanced their spring peak abundances in response to just 3 °C warming, but there was no support for a consumer/resource mismatch in a future climate scenario (Nicolle et al., 2012), in contrast to other mesocosm experiments (Strecker et al., 2004) and long-term studies (Adrian et al., 1999). The few studies of heterotrophic microbes in field mesocosms (Christoffersen et al., 2006; Özen et al., 2012) suggest warming has a much smaller effect than nutrient enrichment, but that it may magnify the positive effect of nutrients on ciliates, bacterioplankton, and nanoflagellates. In warmed pond mesocosms, Shurin et al. (2012) found a greater abundance of pelagic viruses and that increased temperatures magnified the effect of nutrients on bacterioplankton.

Sediment is always present in standing fresh waters, but introducing an inappropriate amount or composition in mesocosms may bias results and influence predictions. Two experiments so far (Moss, 2010; Yvon-Durocher et al., 2010a,b; Fig. 10C) have shown a marked increase (18–35%) in the ratio of community respiration rates to gross photosynthesis with warming by up to 4 °C, as well as increased methane efflux, another important greenhouse gas (Yvon-Durocher et al., 2011b; Fig. 10D). If extrapolated globally, these responses could have immense implications for positive feedbacks in the Earth's future carbon cycle, but as both experiments ran for 1 year (Yvon-Durocher et al., 2010a,b) or less (Moss, 2010), the sediments might not have reached new equilibrial conditions for carbon cycling at the elevated temperatures. Longer-term mesocosm studies could provide further insights here to test the potential effects of substrate-limitation under transient versus equilibrial conditions (Jeppesen et al., 2010a; Liboriussen et al., 2011), especially when complemented with long-term monitoring and modelling of whole systems data and global meta-analysis (Trolle et al., 2012; Yvon-Durocher et al., 2012).

Ideally, the effects of warming in lentic systems would be examined over several years in replicated, very large pond mesocosms (e.g. >1 ha, with shelving depths of up to 10 m). However, controlled heating would be unfeasible in such an experimental design, except perhaps using constructed ponds in geothermal areas such as the Hengill river basin in Iceland (Hannesdóttir et al., 2013; O'Gorman et al., 2012). In the current absence of such idealised systems, mesocosm research will continue to develop in smaller arenas alongside complementary work from models (De Senerpont Domis et al., 2007; Veraart et al., 2011), long-term monitoring (Christensen et al., 2006), space-for-time substitution (Meerhoff et al., 2007; Moss et al., 2004), and paleoecology (Battarbee et al., 2005) in lentic systems.

The difficulties of maintaining controlled conditions in lentic mesocosms also apply to lotic ecosystems, where correlational approaches have also been widely used to infer the effects of a wide range of environmental stressors over the past century (e.g. acidification: Hildrew and Townsend, 1977; Layer et al., 2010, 2011; Ormerod and Edwards, 1987). It is only relatively recently that the effects of climate change have been addressed explicitly in running waters, yet most predictions suggest these ecosystems are especially vulnerable (Barnett et al., 2005; Heino et al., 2009; Ledger et al., 2013a,b; Milly et al., 2005; Parmesan and Yohe, 2003; Vörösmarty et al., 2010; Zwick, 1992). There is huge potential for climate change to generate dangerous synergies with other anthropogenic stressors because running waters have already been exposed to decades of pollution, introductions of exotic species, and habitat modification, which could have compromised their overall resilience (Friberg et al., 2011).

The effects of temperature have been investigated in running waters for decades, but rarely in the context of climate change *per se* (e.g. there is extensive literature on warming via power station effluents; Langford, 1990). More recent work has relied on inference from space-for-time (e.g. Castella et al., 2001; Bonada et al., 2007; Woodward et al., 2010b; cf. Meerhoff et al., 2012) or temporal surveys (Closs and Lake, 1994; Durance and Ormerod, 2007; Harper and Peckarsky, 2006), rather than mesocosm experiments, which have been used far more widely in standing waters. Unfortunately, confounding gradients over time and/or space can undermine these correlational approaches (Durance and Ormerod, 2009; Jacobsen, 2008), whilst warming large bodies of running water is prohibitively expensive and probably explains natural experiments in geothermal areas (Demars et al., 2011; Friberg et al., 2009; Gudmundsdottir et al., 2011b) or across steep altitudinal gradients (e.g. Brown et al., 2007; Lavandier and Décamps, 1983) have been favoured over mesocosm studies.

Ecological responses to the other components of climate change (besides warming) have also been largely ignored in stream mesocosm experiments (Fig. 5A). Correlational data on the effects of flow in running waters, however, are considerable, as it is a well-known central controlling variable in stream ecology (Beniston et al., 2007; Dahm et al., 2003; Daufresne et al., 2007; Dewson et al., 2007; Schindler and Donahue, 2006; Walters and Post, 2011) and a rich literature on the impacts of floods in lotic ecosystems has accrued since the 1980s, when there was a strong focus on understanding the role of flow refugia in determining community structure and dynamics (James et al., 2008; Statzner et al., 1988). Many of these studies are based on correlational field data, although some manipulative experiments and field bioassays were also conducted on the effects of (usually high) flow on the biota and their interactions (Gjerlov et al., 2003; Lancaster, 1996). In contrast, far fewer data are available on the effects of drought (Boulton, 2003) and most are correlational (Lake, 2003), although this is the one aspect of climate change that has been investigated in stream mesocosms.

Habitat loss and fragmentation are often the most obvious consequences of drought events, which alter the distribution and connectivity of freshwater habitats in a predominantly terrestrial landscape. Mimicking low flows associated with drought using flumes has a long tradition in hydrology, and this is now being extended to stream ecology (Hannah et al., 2007; Ledger et al., 2013a,b). There is also a huge body of theory on the ecological effects of habitat loss and fragmentation on (meta)populations and, to a lesser extent, multispecies systems (e.g. Cagnolo et al., 2009; Gonzalez et al., 2011; Saunders et al., 1991) that could be applied to such stream mesocosm experiments in the future.

The responses of biota to drought appear to be relatively amenable to the mesocosm approach, where initial results appear to support the inferences made from survey data, as well as providing mechanistic insights. The impact of drought varies, however, with the organisational level and metric being investigated: for instance, food web connectance is apparently largely invariate despite considerable species turnover, whereas other measures (e.g. food-chain length, species richness) are far more sensitive (Fig. 11C and D; Ledger et al., 2006, 2008, 2013a,b). Impacts on ecosystem processes (e.g. decomposition rates) can be marked (Schlief and Mutz, 2009), supporting findings from laboratory microcosm experiments (Leberfinger et al., 2010). There are suggestions that impacts on some ecosystem processes may be modulated by compensatory community-level responses (e.g. irruptions of small *r*-selected taxa; Ledger et al., 2013a,b). Unfortunately, because climate-change studies in multispecies running-water mesocosms are largely restricted to a handful that have examined the impacts of drought, it is difficult to make meaningful generalisations at this stage.

One specific criticism that may be levelled at stream mesocosm studies is that the channels are often shallow and lack an extensive hyporheic zone (the subsurface and lateral habitat beyond the stream channel itself), which may act as a refugium for small organisms in natural systems. Whether or not this is a major limitation remains a moot point, especially as the role of this refugium may have been overemphasised (Friberg et al., 2011). Thus, although the use of stream mesocosms in climate-change research is still in its infancy, the long tradition of manipulating flow regimes in experimental hydrology gives us cause for optimism: ecologists

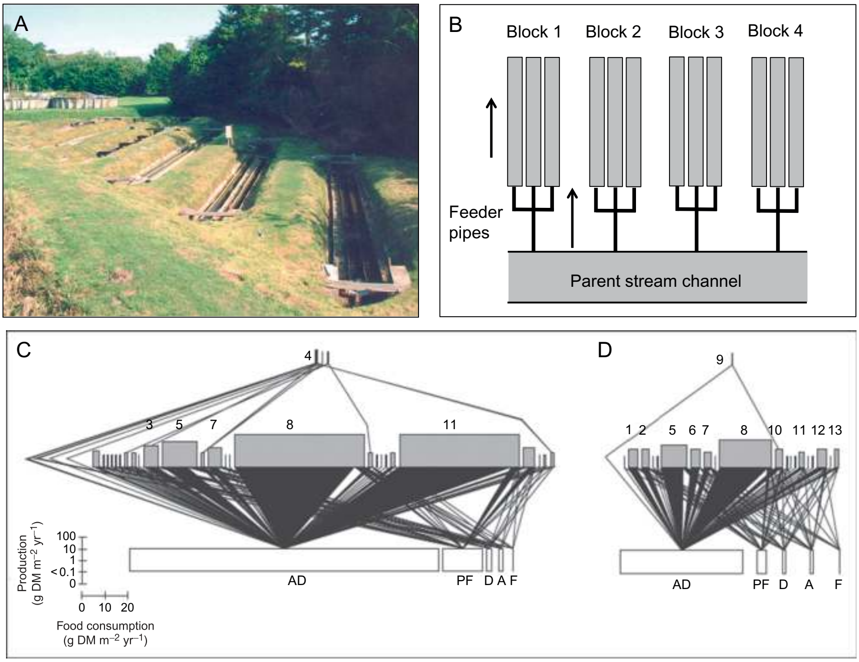

Figure 11 Mesocosm experiments in lotic systems (see Ledger et al., 2013a,b): (A and B) field set-up and (C and D) quantitative food webs for control and the most extreme drought treatment, respectively. Drought reduced the numbers of species, trophic links and biomass flux. The white bars represent basal resources (width is proportional to total consumption) and the grey bars represent consumers (height and width are proportional to mean annual secondary production and ingestion flux, respectively). Black triangles illustrate the total biomass flux to each consumer. Numbers refer to consumer identity, letters to basal resources. *Photo: M. Ledger.*

now need to build on this by considering the biota and components of climate change other than just flow.

2.3. Terrestrial mesocosms and Ecotrons

Some of the earliest syntheses of climate-change impacts on ecosystems came from terrestrial studies (Graham and Grimm, 1990), based on long-term field survey data or shorter-term measures of ecological processes. Whilst initially biassed towards carbon dynamics and primary productivity (e.g. Melillo et al., 1993), studies on individuals, populations, and communities have become increasingly common. These have revealed impacts on body size (e.g. Morgan et al., 1995; Sheridan and Bickford, 2011), range shifts and invasions (e.g. Parmesan et al., 1999; Thomas, 2010), and phenology (e.g. Stevenson and Bryant, 2000; Walther et al., 2002).

Coordinated research programmes have been initiated over the past few decades in a range of countries (e.g. Melillo et al., 1993; Ojima et al., 1991), where the potential role of soil in interactions with climate was recognised from the outset (Dixon and Turner, 1991; Jenkinson et al., 1991). Potential global feedbacks between aboveground vegetation and climate change were summarised by Graetz (1991). Whilst empirical field studies have been a crucial part of describing potential impacts of climate change, the large extents over which these processes operate have challenged ecologists' ability to understand their mechanistic basis, especially given the huge scope for synergies with other stressors (Falkowski et al., 2000). Certain terrestrial ecosystems are considered to be of particular concern in the context of climate change, including those at high latitudes (e.g. Spicer and Chapman, 1990) and agroecosystems (e.g. Goudriaan and Zadoks, 1995), but statistical methods in terrestrial ecology, and in agroecology in particular, have struggled to offer clear insights, as most studies have been primarily correlational.

Although the bias towards inferential surveys still exists, terrestrial ecologists were amongst the first to carry out experiments on the effects of climate. Henry and Molau (1997) warmed large sections of Arctic tundra, and similarly large-scale experiments were undertaken in forest soils (e.g. Melillo et al., 2002). Such studies are logistically challenging, however, and often fail to incorporate critical aspects of future climates, including increases in frequency of extreme events (e.g. Jentsch et al., 2007; Thompson et al., 2013). There are additional difficulties in replicating treatments, particularly when several stressors are being applied in combination. Incorporating multiple stressors is particularly important in these systems, where interactions between temperature, rainfall, and increased atmospheric CO_2 are likely to be significant (Van Peer et al., 2004).

These difficulties have led ecologists to design closed mesocosm systems which operate under more controlled, replicated conditions using an array of approaches, including experimental mesocosms based on artificial or natural systems (e.g. pitcher plant communities; Kitching, 1987), and enclosed 'sections' of natural ecosystems in large-scale and sophisticated Ecotrons (e.g. De Boeck et al., 2011; Lawton, 1996).

Natural soil communities are diverse and variable in both vertical and horizontal dimensions, often over relatively small scales (Schaefer et al., 2010). The distinction between terrestrial microcosms and mesocosms is thus somewhat blurred, but Srivastava et al. (2004) argued that the former are typically smaller than 1 l, whilst the latter may be up to 100,000 l and with a greater capacity to include ecological complexity, whilst retaining a degree of experimental control, in line with our definitions (Appendices 2–4). As in marine systems, mesocosms may prove particularly crucial in terrestrial ecology given the greater difficulty of manipulating whole systems, in contrast with the (relatively) more discrete boundaries of fresh waters. Laboratory mesocosms based on cores taken from fields (Förster et al., 2006) or *in situ* field mesocosms (Scholz-Starke et al., 2011) have long been used in ecotoxicology, and enclosed plots are widely used where surface-dwelling organisms, such as carabid beetles, have been introduced to the experimental arenas (Candolfi et al., 2000; Kampichler et al., 1999; Schaefer et al., 2010). A few model systems, such as the discrete fragmented islands of the flooded Gearagh woodland in southwest Ireland, provide some useful exceptions to this rule where larger 'natural' mesocosms can be used to infer the effects of climate change in the field (McLaughlin et al., 2013).

Responses of terrestrial ecosystems to climate change are difficult to study, in part due to the large scales over which many processes, such as carbon sequestration, operate. Identifying experimental systems that operate at relatively small scales but which have features of larger-scale ecosystems (e.g. complex food web structure, trophic–scaling relationships, species–abundance relationships) is a necessary first step (Srivastava et al., 2004). For instance, the bryosphere, a small-scale ecosystem composed of mosses and their fauna (Lindo et al., 2012), possesses taxonomically diverse food webs that contain a wide range of life-history traits, trophic roles, dispersal abilities, and body sizes (Walter and Proctor, 1999). These systems have provided important ecological insights into the effects of habitat fragmentation on complex communities because treatments can be imposed on scales of just a few centimetres, making them especially amenable for mesocosm (or even microcosm) research (Gonzalez et al., 1998; Staddon et al., 2010; Starzomski and Srivastava, 2007). How well these scale-up to the large-scale fragmentation we see in many natural systems (e.g. Struebig, 2013), however, remains to be seen.

Building on the work of Schneider et al. (2004) and Pollierer et al. (2009), Perdomo et al. (2012) characterised a complex moss–microarthropod food web. A 'landscape' of habitat patches of moss was assembled and exposed to warming and fragmentation (Fig. 12A–D; Perdomo et al., 2012), which had dramatic effects on the food web. Patches which were isolated from large sources were most severely affected by warming and tended to have a food

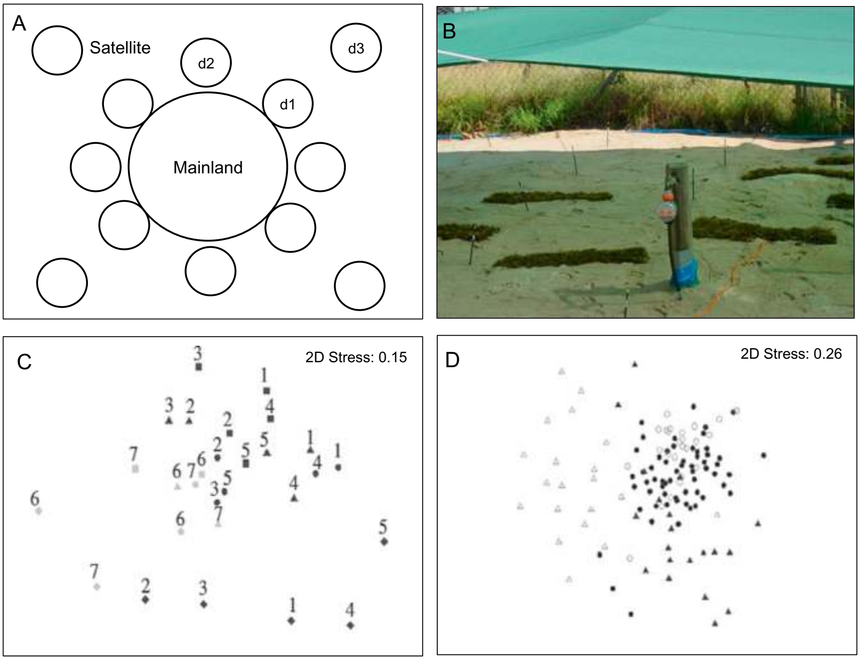

Figure 12 Effects of warming and habitat fragmentation on moss–microarthropod community structure. (A) A circular moss patch ('mainland') taken from the field was placed in the centre of each landscape. Smaller 'satellite' patches were placed at 0 cm = 'd1', 1 cm = 'd2', and 15 cm = 'd3' from the mainland. (B) The experimental landscape. (C) Landscape type affected the resemblance of community composition between mainland (diamonds) and fragments placed at different distances from the mainland (d1, circle; d2, triangles; d3, squares). (D) Unheated moss patches in the experiment (black circles) were more similar to natural winter communities (black triangles) than heated experimental patches (grey circles) and natural summer communities (grey triangles). *Redrawn with permission from Perdomo et al. (2012). Photo: G. Perdomo.*

web structure that differed from any previously described from the field. Heating appeared to destabilise food web structure by causing local extinctions whilst favouring other taxa, resulting in reduced community diversity and evenness. These results showed not only the potential for climate change to alter food webs dramatically in terrestrial ecosystems, but also how 'rescue effects' might buffer those effects when large habitat areas were still present in the landscape. There are some clear echoes here of the food-web effects of drought in stream mesocosms (Ledger et al., 2013a,b), suggesting some common ground in terms of climate-change impacts in otherwise seemingly very different systems.

Mesocosms have been criticised for using ‘unnatural assemblages’, but this is counterbalanced by increased opportunities for control, replication, and repeatability. At the larger end of the spatial scale, the complementary use of experimental set-ups like the ExpeER (Experimentation in Ecosystem Research) network for ecosystem research, which encompasses two Ecotrons (one in the United Kingdom, the other in France) could help to advance terrestrial ecology by introducing even more biocomplexity and realism to the mesocosm approach whilst also being able to control the environment to a very fine level. Ecotrons, several of which are now under construction in a range of countries (e.g. Germany, France, Norway, and Belgium), are highly instrumented sets of chambers designed for ecosystem research under controlled (usually confined) environmental conditions, which allow the simultaneous manipulation and measurement of complex ecological processes in replicated mesocosms.

Although most have been designed to investigate terrestrial systems, many Ecotrons also have the capacity to be adapted to house freshwater and marine systems, or even combinations of the three, which opens up many exciting new possibilities for future research. They are designed to give new insights in the ecological sciences at an intermediate scale between the field and laboratory and to provide a means to integrate experimental research in a way that is not possible with conventional *in situ* approaches. For instance, it is now feasible to set up live data feeds via telemetry that record rainfall and temperature conditions in outside plots, which can be relayed to the often-distant Ecotron facility, where those conditions can be mimicked and replicated in almost real time (De Boeck et al., 2011). Their great Achilles’ heel, though, is the relatively rigid and very expensive infrastructure, which contrasts with the greater flexibility of many other mesocosm approaches. There is a risk, therefore, that the science could become constrained and driven by the method, rather than the most important questions, although these shortcomings can be offset, of course, by using different approaches in parallel.

Field mesocosms and Ecotrons can help to validate mathematical models and accelerate research on ecological processes and functioning (Lawton, 1996). Numerous examples of experiments that bridge the gap between whole systems and physiological studies come from forest ecology. Where several sites lie along environmental gradients (e.g. temperature, rainfall) the ecophysiology and performance of different tree species can be gauged in the field by combining both ‘natural’ and manipulative mesocosm experiments. Mori et al. (2010), for example, enclosed several hundreds of trees across Asia within cylindrical dark chambers with variable heights (from 4 to 9 m); the air in the chamber was circulated and the system was adjusted to a target temperature to measure whole-plant respiration under 'live' observation. In contrast, measuring the belowground root respiration required the use of destructive measures, so partitioning this from aboveground processes can be challenging (Mulder et al., 2012).

Tscherko et al. (2001) investigated the effects of temperature increases on belowground microbial processes (N-mineralisation and denitrification) in both ambient and elevated CO_2 atmospheres. They found that Ecotron soil microbiota responses can be attributed to five key factors: CO_2, temperature, substrate availability, water, and community succession, which acted both as main effects and synergistically with one another, via direct and indirect pathways. This result offers valuable insight into how microbial communities respond to environmental change, specifically in relation to the nitrogen cycle. Perhaps more importantly though, it addressed interactions between different components of climate change, in contrast to earlier work, which tended to address one at a time in isolation from the others (e.g. Jamieson et al., 1998; Post, 1990).

3. WHAT DO WE KNOW SO FAR: GENERALITIES OR IDIOSYNCRATIC EFFECTS?

It may be too early to identify definitive universal responses, if indeed there are any, to climate change among taxa and systems. There are, for example, no obvious common community-level patterns in the changing phenology of plants, invertebrates, and vertebrates in freshwater, marine, or terrestrial habitats, beyond a general advancement in many events and processes with rising temperature (Thackeray et al., 2010). There is, however, far more compelling evidence emerging from mesocosm experiments of consistent effects among other response variables and levels of organisation (cf. Ruess et al., 1993). For instance, there appears to be plenty of scope for redundancy among even distantly related taxa in terms of how they affect process rates. Body size or biomass seems to be key here, with identity and (taxonomic) biodiversity often being less important, at least until systems are degraded to very low levels of species richness (e.g. Naeem, 2001; Ruess et al., 2001). There is also emerging evidence that even though species identities may change markedly, some community properties associated with the size-spectrum and food web structure may be conserved, whereas others may be highly sensitive (Dossena et al., 2012; Ledger et al., 2013a,b; Perdomo et al., 2012). This is in line with empirical observations and theory, such as the general prediction that larger taxa high in the food web are most vulnerable and prone to local extinctions, all else being equal, which has been shown repeatedly in mesocosm studies (Yvon-Durocher et al., 2011c). Finally, there are suggestions from microcosms (cf. Mulder et al., 2006; Rutgers et al., 1989; Tempest, 1970), and increasingly from mesocosms (Naeem, 2001), that systems may move from transient dynamics to more equilibrial conditions at longer timescales, where treatment effects become both more marked and more consistent: thus, we may have been overestimating the apparent idiosyncrasy of certain systems by measuring responses over inadequate timescales (Cardinale et al., 2012). Longer-term, intergenerational studies with repeated sampling should ultimately help to resolve this issue in the future.

Reduced body size across and within species in response to warming is often cited as an almost universal response to climate change, alongside changes in phenology and species range shifts (Angilletta and Dunham, 2004; Daufresne et al., 2009; Sheridan and Bickford, 2011). It has been observed in almost all ectotherms that have been investigated (Daufresne et al., 2009; Walters and Hassall, 2006; but see, O'Gorman et al., 2012; Gardner et al., 2011), yet a precise mechanism remains elusive (Forster and Hirst, 2012, Forster et al., 2011). Most of the direct evidence comes from tightly controlled single-species population studies in microcosms, whereas space-for-time substitution surveys in multispecies assemblages are unable to disentangle the potentially combined effects of temperature and interspecific (e.g. competitive exclusion and predation) interactions, so causality is often impossible to discern (Meerhoff et al., 2012). Mesocosm studies thus provide a useful bridge between these extremes and have provided (at least partial) support for these temperature-size rules based on metabolic theory (e.g. Dossena et al., 2012; Yvon-Durocher et al., 2011b). Indeed, the discrepancies that arise when shifting between different approaches could be just as revealing as the generalities: the exceptions or reversals to the temperature–size relationships reported in microcosms scalings that occur in the field and in mesocosms could be due to the overriding effects of interspecific interactions (Reuman et al., 2013). Mesocosms have been key in providing a new theoretical basis and models for linking community- and ecosystem-level responses to warming in a more general sense, including suggesting how metabolic theory can be applied to connect these levels, via their constituent individual organisms, to explain body-size shifts and other system-level properties (Yvon-Durocher et al., 2010a,b, c, 2011; Yvon-Durocher and Allen, 2012).

The ecosystem-level consequences of shifts in community size structure for the functioning (e.g. carbon sequestration capacity) of ecosystems still remains relatively unexplored. Some studies have attempted to make the connection using metabolic-based theory, providing a means of linking seemingly universal patterns from microcosms to the more idiosyncratic real world (Caron et al., 2009; Harte, 2002; Pascual and Dunne, 2005). Using mesocosms to study pelagic or benthic biogeochemistry represents a substantial increase in scale and biocomplexity from traditional short-term batch incubations. The effects of climate change on some of the key biogeochemical cycles are likely to be multifaceted, complex, and difficult to predict, yet some aspects (increasing CO_2, rising temperatures, strengthened hypoxia, loss of biodiversity, shifts in community structure, etc.) are especially well suited to mesocosm research, particularly when searching for potential generalities across different ecosystems.

Incidences of hypoxia in coastal seas and estuaries, for instance, have increased exponentially over the past 40 years (Diaz and Rosenberg, 2008) and whilst partly symptomatic of eutrophication, longer periods of stratification and rising sea temperatures (one scenario of climate change) will certainly exacerbate it (Weston et al., 2008; Zhang et al., 2010). Riebesell et al. (2008) used mesocosms to show how increases in CO_2 in the ocean's surface waters could increase carbon export from the euphotic layers towards the ocean's interior, which could elevate respiration rates further or even lead to negative feedbacks further offshore (Stramma et al., 2008). A more recent experiment characterised the temperature characteristics of two fundamental aspects of the carbon cycle using freshwater pond mesocosms: carbon fixation by primary production and mineralisation through respiration (Yvon-Durocher et al., 2010a,b). A subsequent global meta-analysis across a diverse array of marine, freshwater, and terrestrial ecosystems revealed a remarkable consistency in the response of respiration to temperature, which also tallied with first principles (Yvon-Durocher et al., 2012) as well as observations from the pond mesocosms and other experiments and surveys (Demars et al., 2011; Perkins et al., 2012). Similarly, impacts of warming on another aspect of the carbon cycle—methane efflux—matched theoretical predictions not just qualitatively, but almost perfectly in quantitative terms (Yvon-Durocher et al., 2011b).

Mesocosms offer a powerful tool for studying and comparing responses to climate change among organisational levels and organismal groups, especially when simultaneous measurements can be made in the same system. For instance, whilst warming caused an order-of-magnitude effect on the body size of the phytoplankton in the Dorset pond mesocosm experiment (Figs. 1E and 10), the benthic fauna were less strongly affected and carbon cycling rates differed by less than 20% (Dossena et al., 2012; Yvon-Durocher et al., 2011a). This lends support to the prevailing (yet largely untested) view that there is considerable scope for taxonomic redundancy in the community to maintain ecosystem functioning, despite potentially huge species turnover. More recently, Yvon-Durocher and Allen (2012) combined these experimental data with new theoretical models to show that seasonal carbon fluxes yielded activation energies similar to those predicted based on the temperature dependencies of individual-level photosynthesis and respiration. In contrast, at the annual timescale, community size structure caused significant changes in ecosystem carbon fluxes: such insights could only be derived through the use of data obtained from field-based mesocosms.

4. FUTURE DIRECTIONS

4.1. New drivers and experimental designs

The current uncertainty about the likely extent of climate change suggests that a greater range of temperatures need to be explored than is usually contemplated (most studies are within a 2–5 °C range of warming), especially when extrapolating to the Arctic, where rates are predicted to be far higher (in the region of 7.5 °C in the next century; IPCC, 2007). A more even coverage of the different components of climate change across habitat types is also needed, as these biases represent some of the most glaring gaps in our knowledge and hinder our ability to generalise (e.g. the focus on hydrology in stream mesocosms vs. acidification in marine systems and warming in standing waters). Whilst some of these biases represent what are perceived to be the major drivers in each habitat, there are clearly other non-scientific reasons (cost, logistics, historical tradition) that need to be rebalanced: for example, warming is likely to be just as important in lotic as it is in lentic freshwaters. This will require greater interdisciplinarity and coordination among research groups and funding bodies, as well as novel experiments.

Further, almost all climate-change mesocosm studies have ignored the critical connections across habitats that exist in nature: headwater stream food webs are fuelled largely by terrestrial leaf-litter, estuarine systems are largely dependent on riverine inputs of nutrients, and lakes are relatively isolated aquatic islands in a terrestrial sea. More imaginative ways of dealing with these interdependencies are needed, and mesocosm approaches in general, and Ecotrons in particular, can help here, as they bring the relevant habitat with them (e.g. marine and freshwater mesocosms can be set up far inland). On a finer scale, there are also important interdependencies between patches of the same habitat type, which need to be considered in the context of the increasing fragmentation and isolation between source and sink habitats in the landscape: this aspect of climate change will modulate the effects of the other components, yet we know very little about such interactive effects (but see, McLaughlin et al., 2013 for a natural experiment). Mesocosm experiments, by their modular nature, could be invaluable here in developing more complex designs that manipulate connectivity, area, and warming effects in the field but which could be impractical in Ecotrons with more rigid infrastructure. Thus, in terms of new drivers and designs to be explored, we clearly need to consider the spatial context (within and among habitat types) as well as the effects of synergistic multiple stressors. There is also a growing awareness of the need to consider different aspects of variation in the environmental drivers of climate change, which parallels a re-appreciation of the need to also consider both the type and amount of variation associated with the responses.

Mesocosms were never conceived 'to mimic the full complexity of nature' (Lawton, 1996), and high levels of control do not necessarily imply a focus on constant conditions, although this has often been the case. Thompson et al. (2013) suggest that climate-change mesocosm studies have taken an overly simplistic approach, with constant 'fixed mean' conditions being adopted alongside conservative assumptions about the range of likely future variation in the driver of interest (usually warming). However, future scenarios of climate change indicate that variation will increase, possibly quite markedly, alongside more gradual shifts in average conditions, with an increase in the frequency, duration, and intensity of extreme events such as floods, droughts, and heat-waves (Thompson et al., 2013). In essence, climate change is a ramped stressor that eventually pushes organisms beyond their typical environmental optima and closer to, or even beyond, their tolerance limits with increasing frequency.

The inherent unpredictability of extreme events means that survey-based studies are unlikely to attract research funding, which is typically short term and risk averse. Routine large-scale biomonitoring data could help here (Thomson et al., 2012), as could studies in which extreme events are tracked through time (Ladle and Bass, 1981; Ledger and Hildrew, 2001; Sponseller et al., 2010; Schlief and Mutz, 2011), but both types of data are correlational and unable to link cause and effect unequivocally. The shortage of such empirical data is not surprising given that extreme events are, by definition, rare and hard to predict. Also, it is difficult to infer the effects of extreme events using a simple space-for-time substitution across a disturbance gradient, as, for example, the community in a stream regularly exposed to disturbance may simply reflect the local filtering of traits selected to deal with such conditions (Gjerlov et al., 2003; Parker and Huryn, 2006): our perception of a disturbance does not necessarily reflect how it is experienced by the biota, and defining it based on absolute values is questionable. It is the return time of an extreme event relative to the generation times and life histories of taxa that is key here (Lytle and Poff, 1994). It is also worth bearing in mind that today's extreme events may be the norm in the future, so the longer-term context is especially important when dealing with this aspect of climate change. Mesocosms are therefore often the best way we can study such impacts in complex systems, especially because correlational data often arise only when an unexpected extreme event has been fortuitously captured by before-and-after sampling. To date, though, this capability has been underused relative to the focus on average effects.

4.2. Future directions: New responses

In terms of the organisational level of the response variables we should measure, there is a strong argument for focusing investigations of temperature effects on ecosystem processes, rather than on community composition. For instance, carbon and nitrogen cycling are likely to be not only more predictable but also of much greater strategic significance than the nuances of community change among the planet's countless taxonomically distinct local assemblages. There is, however, clearly some potential for a stronger community-based focus at the intermediate level between ecosystem processes and taxonomic biodiversity, by considering functional traits, such as body size (Bolnick et al., 2003; Johnson, 2008; Polis, 1984). This is not to say that altered taxonomic biodiversity is not an important response to climate change, rather that there is no strong predictive body of theory supporting it and it is plagued with idiosyncracies that are less of a problem when dealing with other, more parsimonious, ways of viewing ecological phenomena.

In relation to the use of functional traits, populations are often assumed to have fixed, or mean, values, such that all individuals can be readily interchanged. However, numerous ecological and evolutionary mechanisms acting on this intraspecific trait variation can alter community structure and dynamics (see Bolnick et al., 2011 for an overview). The source of trait variation includes both genetic differences and environmental fluctuations, which should drive changes in ecological effects. What is not clear, however, is the relative strength and contribution of the different ecological mechanisms linked to trait variation (Bolnick et al., 2011), or how these shift with changing environmental conditions. Some recent progress has been made with inter-specific competition and trophic interactions, and also with linking ecological and evolutionary dynamics via the food web (Bolnick et al., 2011; Melian et al., 2011; Moya-Larano et al., 2012; Thompson et al., 2013). There is a need now to bring together studies of trait variation and environmental fluctuation within mesocosm experiments and to meld these with appropriate modelling approaches.

Functional traits of taxa are still often only inferred, rather than linked explicitly to an ecosystem process: for instance, body size is widely used as a proxy 'super-trait' to infer impacts on processes from allometric scaling relationships (e.g. Mulder et al., 2012; Perkins et al., 2010). Ideally, a more direct method that links more closely to the process in question would be preferable, as would a more useful measure of functional diversity, and recent advances in microbial molecular ecology, such as the *in situ* application of metagenomics and metatranscriptomics in mesocosm experiments, could provide key new insights here (Bartram et al., 2011; He et al., 2010; Purdy et al., 2010).

Many microcosm experiments have explored the responses of microbes to environmental change, although it is mostly only in the past two decades that these have been done explicitly in the context of climate change (e.g. Beveridge et al., 2010; Petchey et al., 1999). Understanding the functional roles of these organisms *in situ* is far more challenging and until recently they have been confined to a 'black box' in field studies (Purdy et al., 2010; Vandenkoornhuyse et al., 2010), despite early recognition that they are probably the main drivers of most ecosystem processes (e.g. Azam et al., 1983; Finlay and Esteban, 1998; Pomeroy, 1974; Pomeroy et al., 2007). Microscopic diversity is currently at the forefront of DNA-based approaches to taxonomy in marine (Stoeck et al., 2010), freshwater (Medinger et al., 2010), and terrestrial systems (Jumpponen et al., 2010), and recent work has employed the use of molecular techniques to quantify abundance of microbial elements of food webs and to discern their interactions (e.g. via co-occurrence analysis; Alimenti, 2009). These novel techniques are now starting to be applied beyond their initial, rather limited, scope in correlational surveys to more ambitious manipulative field experiments, and there is enormous scope for their application in the emerging generation of new mesocosm-based climate-change studies.

4.3. Future directions: Implementing a more strategic approach to experimental climate-change research

One of the greatest shortcomings in experimental ecology is that it is conducted piecemeal, with (somewhat) different designs, methods, and measures being applied in different places and at different times, usually in short-term snapshots. This largely reflects the financial constraints imposed by national funding bodies, but with the advent of international-scale funding, such as that of the European Research Council and the EU Framework Programmes (George, 2010; Jonckheere, 2007; Wright and Dillon, 2008), much larger coordinated field manipulations, surveys, and bioassays have been conducted in the past 20 years (e.g. Hladyz et al., 2011; Woodward et al., 2012), including the use of mesocosms in multinational climate-change research (George, 2010).

More subtle or complex relationships between drivers and responses are often only apparent at such large scales, which cover sufficiently broad environmental gradients. For instance, a recent pan-European study in 100 streams revealed a complex space-filling response of decomposition rates to nutrient concentrations, which was obscured when decomposed into individual countries because the data became too patchy (Woodward et al., 2012). Without such a coordinated effort, huge amounts of resources and time would have otherwise been wasted simply because each separate study provided only a partial (and often seemingly contradictory) view of the whole. Although this was a field bioassay experiment, the same caveats apply to mesocosm climate-change research, where there are almost as many designs as there are studies, and most are conducted in isolation. This does not invalidate them individually, but it does curtail the realisation of their full potential, as the sum is certainly greater than its parts. Meta-analyses can help here, and a more formal extension of the preliminary explorations of our database (Appendices 2–4) might be a good place to start, although it is a poor substitute for mesocosm experiments designed from the outset to test specific hypotheses *a priori*.

Coordinated international-scale ecological research has been funded in Europe, where some very ambitious projects and programmes (e.g. BIODEPTH, EU-Eurolimpacs, EU-RIVFUNCTION), North America (e.g. LTER), and worldwide (e.g. ITEX), and have been conducted over the past two decades (Foster, 2012; George, 2010; Walkera et al., 2006; Wright and Dillon, 2008). Along the Pacific coast of North America, PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans) has been conducting extensive coordinated studies of the intertidal and subtidal zones for about a decade (e.g. Doney et al., 2011; Iles et al., 2011). At the global scale, for example, ZEN (Zosteria Experimental Network) and KEEN (Kelp Ecosystem Ecology Network) are initiating large collaborative experimental projects. There is clearly a need though, for not just international but intercontinental collaboration: climate change is a global problem that requires global measurements, monitoring programmes, and ecosystem manipulations. There are several levels at which this may be addressed. The first is at the grassroots level, where individual scientists exchange information and share experimental designs to ensure their respective groups obtain synergistic benefits from comparative research. This is potentially difficult in a competitive field with limited funds and huge pressure on individuals to produce high-impact novel research, so the current culture tends to act against this collaborative model. Some common ground may arise from researchers arriving independently at similar solutions to the same questions, or via osmosis, rather than by direct active collaboration from the outset. An example of this is in the pond mesocosm warming experiments set up at different times in the United Kingdom, Denmark, and the United States (Greig et al., 2012; Liboriussen et al., 2005; MacKee et al., 2003; Yvon-Durocher et al., 2010a,b). These used different experimental designs but had some common ground in terms of shared treatments (e.g. ambient vs. 3–5 °C warming) and physical attributes (1000–5000 l), and the focus on community and ecosystem properties.

The next obvious level of integration is for national funding bodies to support larger-scale consortia projects, although these still tend to be contained within their own borders (or at least the funding often is). These can at least set up replicate systems at different sites within the same region, even if installing infrastructure further afield is not possible. Beyond this, there are various bodies that could act as umbrella organisations to facilitate an exchange of ideas and help with planning and coordination via research networks and workshops, whilst not necessarily having to commit huge funds to primary research themselves: rather, they help guide those who want to link up their existing research with other like-minded groups. International bodies, such as the European Science Foundation, European Research Council, the Belmont Forum and G8 Research Councils, the National Center for Ecological Analysis and Synthesis, Diversitas and its successor, and Future Earth, could play significant roles here.

The most challenging level of integration, but the one that offers the greatest rewards, is to have intercontinental, long-term funding for coordinated primary research that combines mesocosms with other approaches. This could be in the form of sustained and standardised (at least within habitats across time and space) biomonitoring in a global set of 'sentinel systems'. These should ideally represent a range of replicated habitats and systems that are especially sensitive to climate change (e.g. tropical coral reefs prone to acidification, arctic peatlands prone to warming, temperate streams exposed to drought). The LTER programmes go some way towards meeting this need, but they often lack experimental components. In addition to continuous survey approaches, coordinated mesocosm experiments should be set up to unpick cause-and-effect relationships at these sites, to help build a clearer global picture of not only the responses to climate change but also the underlying mechanisms. Such data could be central for developing new theory, and vice versa. The current flush of new Ecotron facilities (e.g. Fig. 13) under construction in different countries could link effectively with field mesocosms in this context.

Figure 13 The new Ecotron facility in Montpellier, France. This scale of infrastructure investment provides a critical bridge between field mesocosm experiments and more tightly controlled laboratory microcosm experiments and extends the capabilities of other, earlier Ecotron facilities whilst containing within-system replication (unlike the larger but unreplicated Biosphere 2 project [see Box 1]) *Photos courtesy of CNRS.*

Box 1. The limits of what can be achieved: Biosphere 2 as a cautionary tale

No existing closed environmental facility approaches the size and sophistication of Biosphere 2 (Figure B1), a 13,000 m^2 complex of interconnected, geodesic domes, and vaulted structures which in their original incarnation contained a tropical rain forest, a grassland savannah, a mangrove wetland, a farm, and a salt-water ocean with a wave machine and gravel beach. It was built primarily as an apparatus for the experimental investigation of biogeochemical cycles, whole ecosystems, and life-support systems for space habitation (Nelson et al., 1993) and cost approximately $200 million between 1984 and 1991 (Wolfgang, 1995). Eight humans inhabited Biosphere 2, together with 3800 other introduced species of invertebrates and vertebrates with which it was seeded, and it was hoped that a balanced ecosystem would emerge naturally. However, CO_2 levels rose rapidly and microbial species in the enriched soil also consumed more O_2 than had been predicted, reducing its availability rapidly over time (Severinghaus et al., 1994). Ultimately, most vertebrate and invertebrate species went extinct, including all pollinators, so flowering plants and the crops that were supposed to support the human inhabitants were unable to reproduce. Large populations of ants and cockroaches dominated the invertebrate populations and a host of agricultural pests and pathogens irrupted and wiped out the humans' food supplies. In short, the Biosphere 2 Experiment failed to generate sufficient breathable air, drinkable water, and adequate food for just eight humans, despite an expenditure of $200 million. It serves as a stark reminder for the need to rapidly advance our understanding of how complex multispecies operate and how we might manage them to cater for our needs in an uncertain future (Raffaelli and White, 2013).

These ideas require some ambitious and novel thinking from the scientific and wider communities, especially as research funding is generally shrinking not growing in these austere times, but the amounts of money involved would likely be trivial relative to the longer-term benefits that could accrue. It would also be desirable in any such venture for natural scientists to forge stronger links at the outset with both the physical and social sciences. The latter are better equipped to evaluate ecosystem goods and services that are threatened by climate change, to convey those messages to policymakers, as well as setting up socio-economic–political scenarios for the natural scientists to build into their models and projections (Raffaelli and White, 2013). Climate change has become a truly multidisciplinary science, and one in which mesocosms will play an increasingly important role.

Figure B1 Biosphere 2, USA. Upper panel shows the entire biosphere facility and lower panel shows the simulated ocean ecosystem. *Photos courtesy of C.T. Bannon, CDO Ranching and Development, L.P.*

5. CONCLUSIONS

Whilst we must always bear in mind their obvious limitations (Benton et al., 2007; Cadotte et al., 2005; Fraser and Keddy, 1997), mesocosm experiments will form an integral part of the jigsaw in this field of ecology for the foreseeable future. They will undoubtedly become increasingly crucial elements in the climate-change ecologist's toolbox, particularly where they can be integrated with other, complementary approaches, including field surveys and modelling (Fig. 2). Moving further in this direction will improve our currently limited understanding, as we still cannot predict many of the future ecological consequences of climate change with much certainty.

Creating and maintaining large-scale and coordinated experimental facilities are challenging: equivalent investment in other sciences exists (e.g. particle physics) but these are often perceived to offer more direct economic returns, such as via the development of new technologies (e.g. the development of the Internet as a spin-off from the Large Hadron Collider). Climate-change research does not promise the same immediate socio-economic (or short-term political) benefits, even though the disadvantages of inaction will be vast in terms of their reach, duration, and financial costs on a global scale. Given the complexity of the earth system and how human societies react to change, we may be confined to predicting gross generalities in major processes rather than finer points of how individual species react at local scales, but even that represents a huge and important leap forward from where we are now.

ACKNOWLEDGMENTS

M. D. acknowledges AXA Research Fund for financial support. M. T. and G. W. acknowledge partial financial support of NERC (grant: NE/F004753/1 and NE/D013305/1). M. L., M. T., and G. W. were partly supported by NERC grant NE/J02256X/1. M. M. and E. J. acknowledge ANII Uruguay (grant FCE 2009/2749) and L'Oreal–UNESCO Women in Science award for financial support. We thank Eoin O'Gorman, Wyatt Cross, Mary O'Connor, and an anonymous referee for their comments on an earlier version of the manuscript, which helped us improve it markedly.

APPENDIX 1. PHOTOGRAPHIC CREDITS FOR FIG. 1

(A) Indoor mesocosm experiment used to investigate the effect of warming on plant–herbivore interaction, North Carolina Institute of Marine Sciences, USA (O'Connor, 2009; Photo: M.I. O'Connor); (B) marine mesocosms used to investigate the effect of wave disturbance on intertidal communities, Portaferry, N. Ireland (Photo: N. O'Connor); (C) mesocosms containing plankton assemblages exposed to nutrient enrichment and temperature treatments at the North Carolina Institute of Marine Sciences, USA (O'Connor et al., 2009; Photo: M.I. O'Connor); (D) KOSMOS (Kiel Off-Shore Mesocosms for future Ocean Simulations) developed at the Research Centre for Marine Geosciences (GEOMAR) and deployed south of Bergen, Norway (Photo: U. Riebesell); (E) pond mesocosms used to investigate long-term (5 years) effect of warming on shallow lake ecosystems, Freshwater Biological Association (FBA) River Laboratory, Dorset, UK (Dossena et al., 2012; Yvon-Durocher et al., 2010a,b, 2011a,b;

Photo: M. Dossena); (F) flow-through shallow lake mesocosm system at Silkeborg, Denmark (Christoffersen et al., 2006; Liboriussen et al., 2005, 2011; Photo: E. Jeppesen); (G) experimental flumes at Monash University, Australia, these systems allow fine control on multiple hydrological parameters (Thompson et al., 2013; Photo: R. Thompson); (H) experimental streams used to investigate the effect of drought on stream communities at the FBA River Laboratory, Dorset, UK (Harris et al., 2007; Ledger et al., 2009, 2011, Ledger et al., 2012, Ledger et al., 2013a,b; Woodward et al., 2012; Photo: M. Ledger); (I) tidal marsh mesocosm at the Horn Point Laboratory, Centre for Environmental Science, University of Maryland, USA (Photo: J. Adrian, URL: http://ian.umces.edu/imagelibrary/); (J) terrestrial open-top chambers deployed in the boreal forest of Quebec, Canada, used to investigate the effect of warming and fragmentation on microarthropod communities (Photo: A. Gonzalez); (K) Ecotron facility, Centre National de la Recherche Scientifique, Montpellier, France (Photo: CNRS), these systems allow whole-ecosystem real-time monitoring; and (L) moss patches assembled in an experimental landscape that simulate warming and habitat fragmentation at Monash University, Australia (Perdomo et al., 2012; Photo: G. Perdomo).

APPENDIX 2. LITERATURE SEARCH FOR DATABASE CONSTRUCTION

Literature web searches were conducted within ISI Web of Knowledge using derivations of the following keywords: experiment, mesocosm, microcosm, warming, temperature, climate change, CO_2, pH, drought, population, assemblage, community, and ecosystem. Searches were limited to papers published since 1990 and to the following research areas: environmental science technology, marine freshwater biology, plant science, biodiversity conservation, geochemistry geophysics, oceanography, zoology, entomology, mycology, microbiology, forestry, fisheries, and agriculture. Only research articles were considered in this analysis; reviews, meta-analyses, and methods papers were not considered. The following Boolean search terms were used to identify the categories of study:

- experimental ecological climate-change research that did not use mesocosms: Topic = (experiment*) NOT (mesocosm* OR microcosm*) AND (warm* OR temperature* OR ‘climate change’ OR CO2 OR pH OR drought*) AND (population* OR communit* OR assemblage* OR ecosystem*)

- experimental mesocosms used for research not related to climate change (search terms are: Topic = (experiment*) AND (mesocosm* OR microcosm*) NOT (warm* OR temperature* OR 'climate change' OR CO2 OR pH OR drought*) AND (population* OR communit* OR assemblage* OR ecosystem*)
- experimental mesocosms used for ecological climate change research: Topic = (experiment*) AND (mesocosm* OR microcosm*) AND (warm* OR temperature* OR 'climate change' OR CO2 OR pH OR drought*) AND (population* OR communit* OR assemblage* OR ecosystem*)

The web search of the last category returned 869 articles: these were individually scrutinised to confirm whether or not they conformed to our working definition of a mesocosm experiment. For the purpose of this study, we defined mesocosms as partially or completely enclosed experimental arenas; thus, open-top chambers to partly isolate portions of tundra (e.g. Aerts et al., 2004), enclosures in blocks of peat (e.g. Breeuwer et al., 2010) or within water bodies (e.g. Riebesell et al., 2007) were included, as well as those in discrete containers (e.g. Yvon-Durocher et al., 2010a,b). To distinguish those used in ecological climate-change research from other areas, we only focused on studies in which environmental factors were manipulated to simulate the levels of change in line with IPCC (2007) scenarios. Notable examples of studies that did not conform to our criteria are: laboratory studies conducted on single or few individuals in highly controlled conditions (physiological experiments in chemostat or batch culture, e.g. Finkel et al., 2006; or behavioural studies in very small experimental arenas, e.g. Rall et al., 2010).

APPENDIX 3. CONSTRUCTION OF THE DATABASE

We identified 267 articles that met our search criteria, which were classified as follows:

- Year of publication: 1990 or later.
- Components of climate change manipulated in the experiment. We defined four categories representative of the direct effect of climate change: warming = temperature manipulation trough heating elements, infrared lamps, or passive heating techniques; CO_2 fertilisation = CO_2 level manipulation

resulting in a fertilisation effect on photosynthesis; CO_2 acidification = CO_2 level manipulations resulting in a alteration of the pCO_2 of the system; precipitation patterns = hydrological regime manipulations (e.g. simulation of drought or flooding). Other components of climate change were classified as indirect effects, which included: increased UV radiation; changes in light conditions via modification of shading or water turbidity; changes in quantity and quality of subsidies, simulating consequences of altered run-off; changes in salinity or seawater level. Finally, we classified investigations into synergies between components of climate change and other anthropogenic stressors (e.g. nutrient enrichment, pollution, alterations in habitat type, or biodiversity) as interactive studies.

- Type of systems: M, marine; Le, lentic freshwater; Lo, lotic freshwater; T, terrestrial. Wetlands were defined broadly as systems characterised by an excess of water that permeates the soil, and due to small samples sizes, these were assigned to either lentic freshwaters (e.g. bogs, fens, reedbeds: 19% of this category), or marine systems (e.g. brackish marshes, mangrove swamps: 2% of this category).
- Volume of the experimental enclosure (litres) was binned into three intervals: small ($1–10^2$ l), medium ($10^2–10^4$ l), or large ($>10^4$ l). For field mesocosms that used chambers to manipulate environmental temperature or atmospheric composition, we reported the volume of the chamber; for those that used enclosures to separate soil, sediment, or water we report the volume of the enclosure.
- Absolute duration of the experiment (days) was binned into three intervals: short (<1 month), medium (1 month–1 year), or long (>1 year).
- Relative duration of the experiment (where the lifespan of focal taxa was expressed in days) binned into three intervals: short = lifespan <1 day, medium = 1–100 days, large = >100 days. Lifespan is defined as the time an individual belonging to the focal taxa is expected to live under normal conditions. Focal taxa are defined as either the main object of the study, or, when the studies were conducted on communities or ecosystems, the longest-lived, organism(s) in the system. Lifespan was assigned approximately, as follows: prokaryotic microbes = 10^{-1} days; eukaryotic microbes (e.g. unicellular protists and fungi) = 10^0 days; microinvertebrates (multicellular animals less than 1 mm adult body length) = 10^1 days; macroinvertebrates (multicellular animals between 1 and 50 mm adult body length) = $10^{1.6}$ days; seasonal plants (sporophyte or spermatophyte that accomplish their life cycle within a season) = 10^2 days; large invertebrates (>50 mm adult body length) and vertebrates = 10^{2-3}

days; perennial plants = $10^{3–4}$ days. Given that these are only very coarse approximations there will be many exceptions, but the main aim was to explore broad comparative patterns in the data to identify possible biases, rather than to identify precise patterns within specific studies or ecosystem types.

- The level of biological complexity investigated was defined as: population = the experiment focuses on static (e.g. population density) or dynamic (e.g. growth rate, mortality rate) parameters for a single species; community = the experiment focuses on static (e.g. biomass, density) or dynamic (e.g. species turnover) parameters for a group of species; ecosystem = the experiment focuses on process rates (e.g. production, respiration, nutrient fluxes) measured per unit of ecosystem area or volume. Studies were classified accordingly to the highest level of biological organisation.

APPENDIX 4. ANALYSIS OF THE DATABASE

Two- and three-way contingency tables were constructed to summarise and test for relationships in the information held in the database. These were designed to explore associations among the classes defined using different combinations of grouping factors (i.e. drivers of climate change, ecosystem type, level of biological complexity, spatial scale, and temporal scales), and represented in Figs. 5, 7, and 8. Permutation tests for conditional independence were performed using the double maximum statistic M, which is analogous to χ^2 for the absolute maximum value of the Pearson residual for each cell in a contingency table. We used M, in place of χ^2, because it allows cells that deviate from independence to be identified in multidimensional contingency tables. Association plots were then used to visualise the respective contingency tables, and residual-based shading was used to depict how observed M values departed from the simulated distribution under conditional independence. In association plots, grouping factors (drivers of climate change, ecosystem type, level of biological complexity, spatial, and temporal scales) are represented along either the left, top, or right margin, and each cell of the corresponding contingency table is represented by a rectangle. The height and sign of rectangles are proportional to the corresponding M values, whilst the width is proportional to the square root of the expected frequencies. Shaded cells indicate significant deviation from independence (critical $\alpha = 0.1$). Analyses were conducted

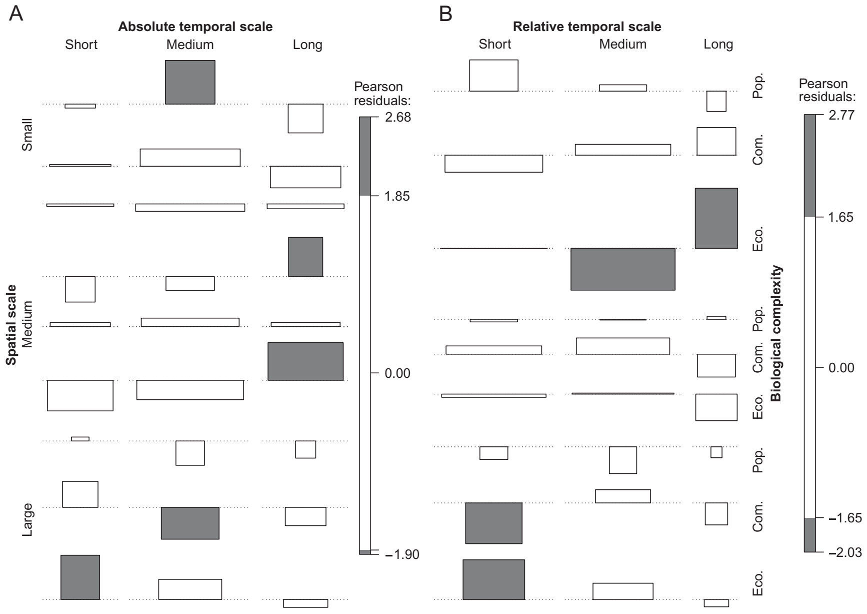

Figure A1 Association plots for Fig. 7A and B. Rectangles represent the classes of three-way contingency tables constructed using the following groups: (A) absolute temporal scale, spatial scale, and levels of biological complexity and (B) relative temporal scale, spatial scale, and levels of biological complexity. Reference bars represent the distribution of the simulated M statistics and the respective positive and negative cut-off values at critical $\alpha = 0.1$. Cells in which the critical *M* value was exceeded (i.e. the observed frequencies are higher/lower than those expected) are shaded in grey; positive and negative *M* values are represented as departure above or below the dashed reference line, respectively.

using the R package **vcd** (Zeileis et al., 2007). Figure 6 represents the association plot derived for the data shown in Fig. 5; Appendix Figs. A1 and A2 are the respective association plots for Figs. 7 and 8.

APPENDIX 5. DATABASE

The database used in the above analyses contained articles that were represented by rows and counted singularly to produce Figs. 4, 6A and B, and 7A and B. Articles containing experiments that manipulated multiple drivers of climate change simultaneously were counted as separate studies to produce Fig. 5A and B. *Sys*, represents the habitat type of the study: M, marine; Le, lentic freshwater; Lo, lotic freshwater; T, terrestrial;

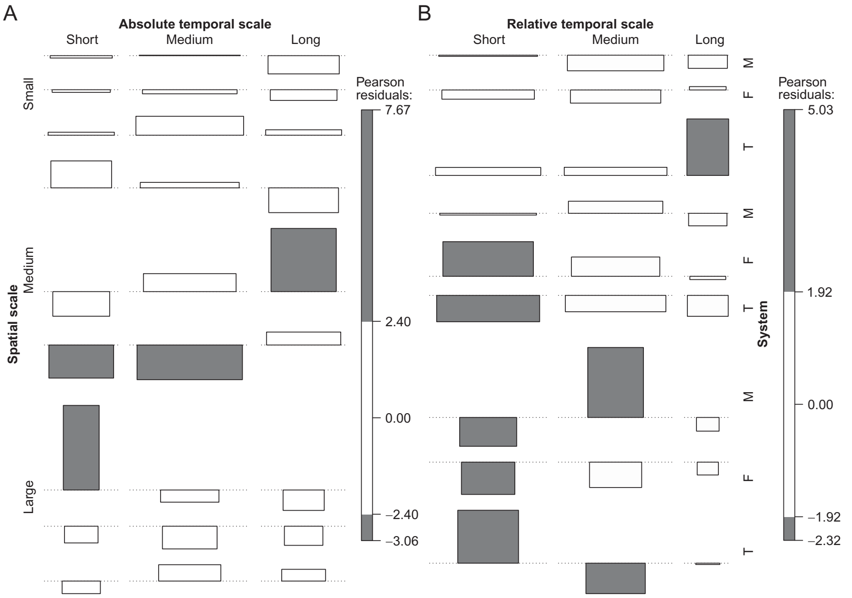

Figure A2 Association plots for Fig. 8A and B. Rectangles represent the classes of three-way contingency tables constructed using the following grouping factors: (A) absolute temporal scale, spatial scale type of ecosystem and (B) relative temporal scale, spatial scale, and type of ecosystem. Ecosystem type are: M, Marine; T, Terrestrial; due to the low level of replication for lentic (Le) ecosystems, these have been merged with lotic (Lo) ecosystems into a single class: F, Freshwater. Reference bars represent the distribution of the simulated M statistics and the respective positive and negative cut-off values at critical $\alpha = 0.1$. Cells in which the critical M value was exceeded (i.e. the observed frequencies are higher/lower than those expected) are shaded in grey; positive and negative M values are represented as departure above or below the dashed reference line, respectively.

Focal taxon represents the main taxonomical group investigated in the study, or, when conducted in multispecies systems, the longest-lived, organism(s) mentioned explicitly in the paper. *Biological complexity* represents the highest level of biological organisation investigated during the experiment (see Appendix 3 for details). *Vol.* represents the volume of the experimental enclosure. *Time* (*abs.*) and *Time* (*rel.*) represent the duration of the experiments in absolute and relative (lifespan) terms, respectively. Volume and time are reported as categorical values: S, small/short; M, medium; L, large/long (see text in Appendix 3 for definitions of the intervals).

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
M	Warming	Microinverts	Comm	M	M	M	Aberle et al. (2007)
M	Warming	Microinverts	Comm	M	M	M	Aberle et al. (2012)
M	Light	Microinverts	Comm	M	M	M	
T	Warming	Peren. plants	Comm	S	L	M	Aerts et al. (2004)
M	CO2_pH	Corals	Pop	S	S	M	Albright et al. (2008)
M	CO2_pH	Peren. plants	Pop	S	S	M	Alexandre et al. (2012)
M	CO2_pH	Eu. micro.	Comm	L	M	M	Allgaier et al. (2008)
M	Warming	Inverts	Eco	S	S	M	Alsterberg et al. (2012)
M	Nutrients	Inverts	Eco	S	S	M	
M	CO2_pH	Corals	Eco	M	S	M	Andersson et al. (2009)
M	CO2_pH	Microinverts	Eco	L	M	S	Antia et al. (2008)
T	CO2_fert	Eu. micro.	Eco	S	L	M	Antoninka et al. (2009)
T	Nutrients	Eu. micro.	Eco	S	L	M	
T	Diversity	Eu. micro.	Eco	S	L	M	
T	CO2_fert	Peren. plants	Comm	L	S	L	Arnone (1997)
T	Nutrients	Peren. plants	Comm	L	S	L	
T	Diversity	pro. micro.	Eco	S	L	M	Ball and Drake (1997)
T	CO2_fert	Seas. plants	Eco	S	M	L	Barnard et al. (2004)
T	CO2_fert	Seas. plants	Eco	S	S	M	Barnard et al. (2005)
T	CO2_fert	Seas. plants	Eco	M	M	L	Barnard et al. (2006)
T	Warming	Seas. plants	Eco	M	M	L	
T	Precipitation	Seas. plants	Eco	M	M	L	
T	Nutrients	Seas. plants	Eco	M	M	L	

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	CO2_fert	Peren. plants	Eco	L	S	L	Barron-Gafford et al. (2005)
T	Warming	Peren. plants	Eco	L	S	M	Barron-Gafford et al. (2007)
T	Precipitation	Peren. plants	Eco	L	S	M	
Le	Nutrients	Peren. plants	Eco	M	S	L	Barker et al. (2008)
T	Warming	Peren. plants	Comm	S	S	L	Bates et al. (2005)
T	Precipitation	Peren. plants	Comm	S	S	L	
Le	Warming	Inverts	Eco	M	M	M	Baulch et al. (2005)
M	CO2_pH	Eu. micro.	Eco	L	M	M	Bellerby et al. (2008)
Le	Warming	Microinverts	Comm	M	M	M	Berger et al. (2010)
T	Precipitation	Pro. micro.	Eco	S	L	S	Bérard et al. (2012)
T	CO2_fert	Peren. plants	Eco	S	S	L	Berntson and Bazzaz (1998)
T	Nutrients	Peren. plants	Eco	S	S	L	
T	CO2_fert	Seas. plants	Eco	M	M	M	Bezemer et al. (1998)
T	Warming	Seas. plants	Eco	M	M	M	
M	CO2_pH	Inverts	Pop	S	S	S	Bibby et al. (2007)
T	CO2_fert	Pro. micro.	Eco	L	L	L	Blagodatskaya et al. (2010)
T	Precipitation	Peren. plants	Eco	S	S	M	Blodau and Moore (2003)
T	Precipitation	Peren. plants	Eco	S	S	M	Blodau et al. (2004)
T	Diversity	Peren. plants	Eco	S	S	M	
T	Precipitation	Peren. plants	Eco	S	S	M	Bloor et al. (2009)
T	CO2_fert	Peren. plants	Eco	S	S	M	
T	Nutrients	Peren. plants	Eco	S	S	M	
Le	Warming	Peren. plants	Eco	M	S	L	Boros et al. (2011)
Le	Nutrients	Peren. plants	Eco	M	S	L	

Continued

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	Nutrients	Eu. micro.	Eco	S	L	L	Bradford et al. (2008a)
T	Nutrients	Eu. micro.	Eco	S	L	L	Bradford et al. (2008b)
Le	Precipitation	Peren. plants	Comm	S	S	L	Breeuwer et al. (2009)
T	Nutrients	Peren. plants	Eco	S	S	L	Breeuwer et al. (2010)
T	Precipitation	Peren. plants	Eco	S	S	L	
Le	Warming	Peren. plants	Eco	M	S	L	Bridgham et al. (2008)
Le	Precipitation	Peren. plants	Eco	M	S	L	
Le	Diversity	Peren. plants	Eco	M	S	L	
T	Warming	Peren. plants	Eco	M	S	M	Bridgham et al. (1999)
T	Warming	Inverts	Eco	S	M	L	Briones et al. (2009)
Le	Warming	Fish	Comm	M	S	M	Buckel et al. (1995)
Le	Salinity	Fish	Comm	M	S	M	
Le	Precipitation	Peren. plants	Comm	M	S	M	Bucak et al. (2012)
Le	Diversity	Peren. plants	Comm	M	S	M	
Le	Warming	Eu. micro.	Comm	S	L	L	Burgmer and Hillebrand (2011)
T	Warming	Pro. micro.	Eco	S	L	S	Butenschoen et al. (2011)
T	Precipitation	Pro. micro.	Eco	S	L	S	
T	Diversity	Pro. micro.	Eco	S	L	S	
T	Warming	Seas. plants	Pop	S	S	M	Campbell et al. (1995)
T	CO2_fert	Seas. plants	Pop	S	S	M	
T	CO2_fert	Seas. plants	Eco	S	M	M	Campbell et al. (1997)
T	Precipitation	Seas. plants	Eco	S	M	M	
Le	Diversity	Inverts	Eco	S	M	M	Carrera et al. (2009)
Le	Warming	Inverts	Eco	S	M	M	
T	CO2_fert	Seas. plants	Comm	M	S	M	Chen et al. (2007)
T	Diversity	Seas. plants	Comm	M	S	M	

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	CO2_fert	Seas. plants	Eco	L	S	M	Cheng et al. (2000a)
T	CO2_fert	Seas. plants	Eco	L	S	M	Cheng et al. (2000b)
M	CO2_fert	Seas. plants	Eco	S	M	L	Cherry et al. (2009)
M	Sea rise	Seas. plants	Eco	S	M	L	
Le	Run-off	Microinverts	Comm	M	M	M	Christensen et al. (2006)
Le	Warming	Microinverts	Comm	M	M	M	
Le	CO2_pH	Microinverts	Comm	M	M	M	
Le	Warming	Eu. micro.	Pop	M	L	L	Christoffersen et al. (2006)
Le	Nutrients	Eu. micro.	Pop	M	L	L	
T	Warming	Inverts	Eco	S	M	M	Cole et al. (2002)
T	Diversity	Inverts	Eco	S	M	M	
T	Warming	Microinverts	Comm	S	M	M	Dam et al. (2012)
M	CO2_pH	Inverts	Comm	S	S	M	Dashfield et al. (2008)
M	Diversity	Inverts	Comm	S	S	M	
Le	Warming	Eu. micro.	Pop	S	M	M	Domis et al. (2007)
M	CO2_pH	Eu. micro.	Eco	L	M	S	Delille (2005)
Le	Precipitation	Peren. plants	Eco	S	S	M	Deppe et al. (2010)
Le	Diversity	Peren. plants	Eco	S	S	M	
T	CO2_fert	Seas. plants	Comm	S	M	M	Díaz et al. (1998)
M	Warming	Eu. micro.	Comm	M	M	S	Domaizon et al. (2012)
M	Light	Eu. micro.	Comm	M	M	S	
T	Warming	Peren. plants	Comm	M	S	L	Dorrepaal et al. (2003)
Le	Warming	Inverts	Eco	M	M	L	Dossena et al. (2012)
T	Warming	Seas. plants	Comm	S	S	M	Dunnett and Grime (1999)

Continued

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	CO2_fert	Seas. plants	Eco	S	M	L	Edwards et al. (2005)
T	Diversity	Seas. plants	Eco	S	M	L	
T	Nutrients	Seas. plants	Eco	S	M	L	
T	CO2_fert	Seas. plants	Eco	S	M	L	Edwards et al. (2006)
T	Nutrients	Seas. plants	Eco	S	M	L	
M	CO2_pH	Microinverts	Eco	L	M	M	Egge et al. (2009)
M	Diversity	Seas. plants	Comm	M	S	M	Ehlers et al. (2008)
M	Warming	Seas. plants	Comm	M	S	M	
T	Warming	Inverts	Comm	S	S	M	Eisenhauer et al. (2012)
T	Diversity	Inverts	Comm	S	S	M	
M	Warming	Inverts	Comm	S	S	M	Eklöf et al. (2012)
M	CO2_pH	Inverts	Comm	S	S	M	
Le	Warming	Microinverts	Comm	M	M	M	Ekvall and Hansson (2012)
Le	Light	Microinverts	Comm	M	M	M	
M	Warming	Fish	Comm	M	S	S	Elliott and Leggett (1997)
M	CO2_pH	Eu. micro.	Eco	L	M	S	Engel et al. (2005)
M	CO2_pH	Microinverts	Eco	L	M	S	Engel et al. (2008)
M	Warming	Macroinverts	Eco	M	S	M	Eriksson Wilkund et al. (2009)
M	Diversity	Macroinverts	Eco	M	S	M	
T	Warming	Seas. plants	Eco	S	S	M	Faubert et al. (2011)
T	Precipitation	Seas. plants	Eco	S	S	M	
T	Precipitation	Seas. plants	Eco	M	M	M	Fay et al. (2008)
M	CO2_pH	Fish	Comm	M	S	S	Ferrari et al. (2011)
Le	Warming	Fish	Comm	M	S	L	Feuchtmayr et al. (2007)
Le	Nutrients	Fish	Comm	M	S	L	
Le	Diversity	Fish	Comm	M	S	L	

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
Le	Warming	Fish	Eco	M	S	M	Feuchtmayr et al. (2009)
Le	Nutrients	Fish	Eco	M	S	M	
Le	Diversity	Fish	Eco	M	S	M	
Le	Warming	Microinverts	Eco	M	M	M	Feuchtmayr et al. (2010)
Le	Nutrients	Microinverts	Eco	M	M	M	
Le	Warming	Fish	Comm	M	S	M	Fey and Cottingham (2012)
Le	Diversity	Fish	Comm	M	S	M	
Le	Warming	Microinverts	Eco	M	M	M	Flanagan et al. (2006)
Le	Diversity	Microinverts	Eco	M	M	M	
Le	Warming	Inverts	Comm	M	S	M	Flanagan and McCauley (2010)
Le	Warming	Microinverts	Comm	S	M	M	Fox and Morin (2001)
Le	Diversity	Microinverts	Comm	S	M	M	
M	Run-off	Pro. micro.	Eco	M	L	M	Fulweiler et al. (2007)
M	Warming	Microinverts	Comm	M	M	L	Gaedke et al. (2010)
M	Light	Microinverts	Comm	M	M	L	
M	Warming	Peren. plants	Pop	S	S	M	García et al. (2012)
T	Warming	Eu. micro.	Eco	S	L	M	Goldberg et al. (2008)
Le	Warming	Microinverts	Comm	M	M	M	Graham and Vinebrooke (2009)
Le	Run-off	Microinverts	Comm	M	M	M	
Le	Warming	Fish	Eco	M	S	M	Greig et al. (2012)
Le	Nutrients	Fish	Eco	M	S	M	
Le	Diversity	Fish	Eco	M	S	M	
T	Warming	Seas. plants	Comm	S	M	L	Grime et al. (2000)
T	Precipitation	Seas. plants	Comm	S	M	L	

Continued

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
Le	Warming	Microinverts	Comm	S	M	L	Grover et al. (2000)
Le	Diversity	Microinverts	Comm	S	M	L	
T	Warming	Peren. plants	Eco	S	S	S	Grogan et al. (2004)
M	CO2_pH	Eu. micro.	Comm	L	M	S	Grossart et al. (2006)
T	Warming	Pro. micro.	Eco	S	M	S	Grote et al. (2010)
T	Precipitation	Pro. micro.	Eco	S	M	S	
M	Warming	Inverts	Pop	S	M	M	Gutow and Franke (2001)
M	CO2_pH	Inverts	Comm	S	M	M	Hale et al. (2011)
M	Warming	Inverts	Comm	S	M	M	
Lo	CO2_pH	Inverts	Eco	M	M	M	Hargrave et al. (2009)
T	CO2_fert	Seas. plants	Pop	M	M	L	Hattas et al. (2005)
Le	Salinity	Eu. micro.	Eco	M	M	M	Herbst and Blinn (1998)
M	Warming	Peren. plants	Comm	S	S	M	Hillebrand (2011)
M	Nutrients	Peren. plants	Comm	S	S	M	
M	Warming	Eu. micro.	Comm	S	L	M	Hillebrand et al. (2012)
M	Light	Eu. micro.	Comm	S	L	M	
T	CO2_fert	Peren. plants	Pop	M	S	L	Hobbie and Gregg (2002)
T	Warming	Peren. plants	Pop	M	S	L	
T	CO2_fert	Peren. plants	Eco	M	S	L	Hobbie et al. (2004)
T	Warming	Peren. plants	Eco	M	S	L	
T	CO2_fert	Pro. micro.	Eco	S	L	S	Hodge et al. (1998)
M	CO2_pH	Corals	Comm	S	S	M	Hofmann et al. (2012)
M	Warming	Microinverts	Eco	M	M	M	Hoppe et al. (2008)

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
M	CO2_pH	Eu. micro.	Eco	L	M	S	Hopkins et al. (2010)
T	CO2_fert	Seas. plants	Eco	S	S	M	Hu et al. (2005)
T	CO2_fert	Seas. plants	Eco	S	S	M	Hu et al. (2005)
M	Warming	Corals	Comm	S	S	M	Hueerkamp et al. (2001)
T	Warming	Inverts	Comm	S	M	M	Huhta and Hänninen (2001)
T	Precipitation	Inverts	Comm	S	M	M	
T	CO2_fert	Seas. plants	Eco	L	S	M	Hui et al. (2001)
T	Precipitation	Seas. plants	Comm	S	S	S	Innocenti et al. (2011)
M	Warming	Microinverts	Pop	M	M	M	Isla et al. (2008)
M	Warming	Inverts	Pop	S	M	M	Jacobson et al. (2008)
M	Pollutant	Inverts	Pop	S	M	M	
T	Warming	Eu. micro.	Comm	S	M	M	Jassey et al. (2011)
Le	Warming	Eu. micro.	Comm	S	M	M	Jiang and Kulczycki (2004)
Le	Diversity	Eu. micro.	Comm	S	M	M	
T	CO2_fert	Seas. plants	Comm	M	M	M	Joel et al. (2001)
T	Nutrients	Seas. plants	Comm	M	M	M	
T	Precipitation	Seas. plants	Eco	S	S	M	Johnson et al. (1996)
T	Warming	Seas. plants	Eco	S	S	M	
T	CO2_fert	Seas. plants	Comm	M	S	M	Johnson et al. (2003)
T	Diversity	Seas. plants	Comm	M	S	M	
T	Nutrients	Seas. plants	Comm	M	S	M	
M	CO2_pH	Peren. plants	Pop	M	S	M	Jokiel et al. (2008)

Continued

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	Warming	Seas. plants	Eco	S	M	M	Jonasson et al. (2004)
T	Run-off	Seas. plants	Eco	S	M	M	
T	Diversity	Seas. plants	Eco	S	M	M	
T	Warming	Seas. plants	Eco	S	S	S	Joseph and Henry (2008)
T	Precipitation	Peren. plants	Eco	S	S	S	Judd and Kling (2002)
T	Diversity	Peren. plants	Eco	S	S	S	
Le	Run-off	Microinverts	Eco	S	M	S	Kankaala et al. (2010)
T	CO2_fert	Seas. plants	Comm	S	M	M	Kao-Kniffin and Balser (2007)
T	Diversity	Seas. plants	Comm	S	M	M	
T	Nutrients	Seas. plants	Comm	S	M	M	
Le	Warming	Peren. plants	Eco	M	S	L	Keller et al. (2004)
Le	Precipitation	Peren. plants	Eco	M	S	L	
Le	Diversity	Peren. plants	Eco	M	S	L	
T	CO2_fert	Seas. plants	Eco	S	M	M	Kettunen et al. (2006)
T	Precipitation	Seas. plants	Eco	S	M	M	
M	CO2_pH	Eu. micro.	Comm	M	M	S	Kim et al. (2006)
M	Warming	Microinverts	Comm	M	M	L	Klauschies et al. (2012)
M	Light	Microinverts	Comm	M	M	L	
M	Nutrients	Microinverts	Comm	M	M	L	
M	Warming	Peren. plants	Pop	M	S	M	Koch et al. (2007)
M	Nutrients	Peren. plants	Pop	M	S	M	
T	Diversity	Seas. plants	Comm	S	S	M	Kohler et al. (2010)
T	Precipitation	Seas. plants	Comm	S	S	M	
T	CO2_fert	Seas. plants	Comm	S	S	M	
Le	Warming	Eu. micro.	Comm	M	L	L	Kratina et al. (2012)
Le	Nutrients	Eu. micro.	Comm	M	L	L	
Le	Diversity	Eu. micro.	Comm	M	L	L	

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
M	CO2_pH	Peren. plants	Comm	M	S	M	Kuffner et al. (2007)
M	CO2_pH	Corals	Eco	L	S	S	Langdon et al. (2003)
M	CO2_pH	Corals	Eco	M	S	S	
M	Warming	Corals	Eco	M	S	S	Langdon (2005)
M	Nutrients	Corals	Eco	M	S	S	
M	CO2_fert	Seas. plants	Eco	M	S	M	Langley et al. (2009)
M	Nutrients	Seas. plants	Eco	M	S	M	
M	CO2_pH	Peren. plants	Eco	M	S	S	Leclercq et al. (2000)
M	CO2_pH	Peren. plants	Eco	M	S	S	Leclercq et al. (2002)
M	Diversity	Peren. plants	Eco	M	S	S	
Lo	Precipitation	Inverts	Eco	M	M	L	Ledger et al. (2011)
M	Warming	Microinverts	Eco	M	M	M	Lassen et al. (2010)
M	Warming	Microinverts	Eco	M	M	M	Lewandowska and Sommer (2010)
M	Precipitation	Microinverts	Eco	M	M	M	
Le	Warming	Fish	Eco	M	M	L	Liboriussen et al. (2011)
Le	Nutrients	Fish	Eco	M	M	L	
T	CO2_fert	Peren. plants	Eco	L	S	M	Lin et al. (1998)
T	CO2_fert	Peren. plants	Eco	L	S	M	Lin et al. (1999)
T	CO2_fert	Peren. plants	Eco	L	S	M	Lin et al. (1999)
T	CO2_fert	Peren. plants	Eco	M	S	L	Lin et al. (2001)
T	Warming	Peren. plants	Eco	M	S	L	
M	Warming	Eu. micro.	Comm	M	M	S	Lionard et al. (2012)
M	Light	Eu. micro.	Comm	M	M	S	

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Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	CO2_fert	Seas. plants	Eco	M	M	M	Luo et al. (1996)
T	CO2_fert	Seas. plants	Eco	L	S	M	Luo et al. (2000)
Le	Warming	Inverts	Comm	M	S	S	MacPhee et al. (2011)
Le	Diversity	Inverts	Comm	M	S	S	
T	CO2_fert	Seas. plants	Comm	S	S	M	Maestre et al. (2005)
T	Nutrients	Seas. plants	Comm	S	S	M	
T	Nutrients	Seas. plants	Pop	S	S	M	Maestre and Reynolds (2006a)
T	CO2_fert	Seas. plants	Pop	S	S	M	
T	Diversity	Seas. plants	Pop	S	S	M	
T	CO2_fert	Seas. plants	Pop	S	S	M	Maestre and Reynolds (2006b)
T	Nutrients	Seas. plants	Pop	S	S	M	
T	CO2_fert	Seas. plants	Pop	S	S	M	Maestre et al. (2007)
T	Nutrients	Seas. plants	Pop	S	S	M	
T	Diversity	Seas. plants	Pop	S	S	M	
T	CO2_fert	Seas. plants	Comm	S	S	M	Maestre and Reynolds (2007)
T	Diversity	Seas. plants	Comm	S	S	M	
M	Nutrients	Eu. micro.	Comm	L	M	S	Martinez-Martinez et al. (2006)
M	CO2_pH	Peren. plants	Eco	S	S	L	Martin and Gattuso (2009)
M	Warming	Peren. plants	Eco	S	S	L	
Le	Warming	Fish	Comm	M	S	L	McKee et al. (2002)
Le	Nutrients	Fish	Comm	M	S	L	
Le	Diversity	Fish	Comm	M	S	L	
Le	Warming	Fish	Comm	M	S	L	McKee et al. (2003)
Le	Nutrients	Fish	Comm	M	S	L	
Le	Diversity	Fish	Comm	M	S	L	

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
M	CO2_fert	Peren. plants	Comm	S	S	L	McKee and Rooth (2008)
M	Diversity	Peren. plants	Comm	S	S	L	
M	Nutrients	Peren. plants	Comm	S	S	L	
T	Precipitation	Eu. micro.	Comm	S	L	M	McLean and Huhta (2000)
M	CO2_pH	Eu. micro.	Comm	L	M	S	Meakin and Wyman (2011)
T	Warming	Seas. plants	Eco	M	M	L	Menge and Field (2007)
T	Nutrients	Seas. plants	Eco	M	M	L	
T	Precipitation	Seas. plants	Eco	M	M	L	
T	Nutrients	Peren. plants	Eco	M	S	M	Mikan et al. (2000)
T	CO2_fert	Peren. plants	Eco	M	S	M	
M	Precipitation	Eu. micro.	Comm	S	M	S	Miller et al. (2008)
Le	Warming	Inverts	Pop	S	M	M	Moenickes et al. (2011)
Le	Nutrients	Peren. plants	Eco	S	S	M	Moore et al. (2005)
M	Habitat change	Microinverts	Pop	S	M	M	Mora et al. (2007)
M	Diversity	Microinverts	Pop	S	M	M	
M	Warming	Microinverts	Pop	S	M	M	
Le	Warming	Fish	Comm	M	S	M	Moran et al. (2010)
Le	Nutrients	Fish	Comm	M	S	M	
Le	Warming	Fish	Comm	M	S	L	Moss et al. (2003)
Le	Nutrients	Fish	Comm	M	S	L	
Le	Diversity	Fish	Comm	M	S	L	
M	Warming	Microinverts	Eco	M	M	S	Müren et al. (2005)
Le	Diversity	Fish	Comm	M	S	M	Netten et al. (2010)
Le	Nutrients	Fish	Comm	M	S	M	
Le	Warming	Fish	Comm	M	S	M	

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Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
Le	Warming	Eu. micro.	Comm	S	M	S	Newsham and Garstecki (2007)
Le	Diversity	Eu. micro.	Comm	S	M	S	
Le	Warming	Microinverts	Comm	M	M	M	Nicolle et al. (2012)
Le	Run-off	Microinverts	Comm	M	M	M	
M	CO2_pH	Eu. micro.	Comm	S	M	S	Nielsen et al. (2010)
T	CO2_fert	Seas. plants	Comm	S	M	L	Niklaus et al. (1998)
T	Nutrients	Seas. plants	Comm	S	M	L	
T	Nutrients	Seas. plants	Eco	M	M	L	Niu et al. (2010)
T	Diversity	Seas. plants	Eco	M	M	L	
Le	Light	Peren. plants	Eco	M	S	M	Noormets et al. (2004)
T	Warming	Pro. micro.	Comm	S	L	S	Norris et al. (2002)
M	Diversity	Microinverts	Comm	S	M	M	Norberg (1998)
M	Light	Microinverts	Comm	S	M	M	
M	Warming	Microinverts	Comm	S	M	M	
T	Nutrients	Seas. plants	Eco	L	M	M	Obrist et al. (2003)
M	Warming	Eu. micro.	Comm	S	S	L	O'Connor et al. (2009)
	Nutrients						
T	CO2_fert	Peren. plants	Eco	M	S	L	Olszyk et al. (2001)
T	Diversity	Inverts	Comm	S	M	M	Ott et al. (2012)
T	Warming	Inverts	Comm	S	M	M	
Le	Nutrients	Microinverts	Comm	M	M	M	Özen et al. (2012)
Le	Warming	Microinverts	Comm	M	M	M	
Le	Light	Microinverts	Comm	S	M	M	Pajares et al. (2012)
Le	Warming	Microinverts	Comm	S	M	M	

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
M	CO2_pH	Peren. plants	Pop	M	S	L	Palacios and Zimmerman (2007)
Le	Warming	Peren. plants	Eco	M	S	L	Pastor et al. (2003)
Le	Precipitation	Peren. plants	Eco	M	S	L	
Le	Warming	Peren. plants	Comm	M	S	M	Patrick et al. (2012)
M	CO2_pH	Microinverts	Comm	L	M	M	Paulino et al. (2008)
M	Warming	Macroinverts	Pop	M	S	M	Pearce et al. (1998)
T	Precipitation	Peren. plants	Eco	L	S	M	Pegoraro et al. (2005a)
T	CO2_fert	Peren. plants	Eco	L	S	M	
T	CO2_fert	Peren. plants	Eco	L	S	L	Pegoraro et al. (2005b)
T	Precipitation	Peren. plants	Eco	L	S	L	
T	Warming	Inverts	Comm	S	M	M	Perdomo et al. (2012)
T	Habitat change	Inverts	Comm	S	M	M	
Lo	Warming	Eu. micro.	Eco	S	S	S	Perkins et al. (2012)
Le	Warming	Eu. micro.	Eco	S	M	L	Petchey et al. (1999)
Le	Diversity	Eu. micro.	Eco	S	M	L	
M	Warming	Eu. micro.	Comm	M	M	S	Piontek et al. (2009)
T	CO2_fert	Peren. plants	Eco	S	S	L	Possell et al. (2004)
T	Nutrients	Peren. plants	Eco	S	S	L	
T	CO2_fert	Seas. plants	Comm	M	M	L	Rämö et al. (2006)
T	Precipitation	Peren. plants	Eco	L	S	M	Rascher et al. (2004)
Le	Warming	Inverts	Comm	S	M	M	Reynolds and Benke (2005)

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Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
M	CO2_pH	Microinverts	Eco	L	M	S	Riebesell et al. (2007)
M	Diversity	Eu. micro.	Pop	S	M	S	Roger et al. (2012)
M	Salinity	Eu. micro.	Pop	S	M	S	
M	Warming	Eu. micro.	Pop	S	M	S	
T	CO2_fert	Peren. plants	Eco	L	S	M	Rosenthal (1998)
M	Warming	Microinverts	Comm	M	S	S	Rüger and Sommer (2012)
M	CO2_pH	Peren. plants	Eco	S	S	M	Russell et al. (2009)
M	Nutrients	Peren. plants	Eco	S	S	M	
M	Warming	Macroinverts	Comm	M	S	M	Sanford (2002)
M	Diversity	Macroinverts	Comm	M	S	M	
M	Run-off	Inverts	Eco	S	S	M	Sanz-Lázaro et al. (2011)
M	Warming	Inverts	Eco	S	S	M	
M	CO2_pH	Microinverts	Comm	L	M	S	Schulz et al. (2008)
Le	Precipitation	Inverts	Eco	S	S	S	Schlief and Mutz (2009)
Le	Warming	Inverts	Comm	M	M	M	Sebastian et al. (2012)
T	CO2_fert	Seas. plants	Eco	M	M	L	Shaw et al. (2002)
T	Warming	Pro. micro.	Comm	S	M	S	Sharma et al. (2006)
Le	Nutrients	Macroinverts	Comm	M	M	L	Shurin et al. (2012)
Le	Diversity	Macroinverts	Comm	M	M	L	
Le	Warming	Macroinverts	Comm	M	M	L	
M	Warming	Microinverts	Comm	M	M	M	Sommer et al. (2007)
M	Light	Microinverts	Comm	M	M	M	
M	Warming	Microinverts	Comm	M	M	M	Sommer and Lengfellner (2008)
M	Light	Microinverts	Comm	M	M	M	

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
M	Warming	Microinverts	Comm	M	M	M	Sommer and Lewandowska (2011)
M	Diversity	Microinverts	Comm	M	M	M	
M	Warming	Microinverts	Comm	M	M	M	Sommer et al. (2012)
M	Diversity	Microinverts	Comm	M	M	M	
M	Light	Microinverts	Comm	M	M	M	
M	Warming	Inverts	Comm	S	S	M	Sorte et al. (2010)
M	Diversity	Inverts	Comm	S	S	M	
M	Warming	Macroinverts	Comm	S	S	M	
T	Precipitation	Seas. plants	Eco	M	M	M	Saint Clair et al. (2009)
T	Diversity	Seas. plants	Eco	M	M	M	
T	Nutrients	Seas. plants	Eco	M	M	M	
T	CO2_fert	Seas. plants	Comm	S	M	M	Stöcklin et al. (1997)
T	CO2_fert	Seas. plants	Comm	S	M	L	Stöcklin and Körner (1999)
T	Nutrients	Seas. plants	Comm	S	M	L	
T	Diversity	Seas. plants	Comm	S	M	L	
Le	Warming	Microinverts	Comm	M	M	M	Strecker et al. (2004)
M	CO2_pH	Microinverts	Comm	L	M	S	Suffrian et al. (2008)
T	Warming	Macroinverts	Eco	S	S	M	Sulkava and Huhta (2003)
T	Diversity	Macroinverts	Eco	S	S	M	
M	Light	Peren. plants	Comm	M	S	M	Swanson and Fox (2007)
M	Warming	Peren. plants	Comm	M	S	M	
M	CO2_pH	Microinverts	Comm	L	M	S	Tanaka et al. (2008)
M	Warming	Microinverts	Eco	M	M	M	Taucher et al. (2012)
M	CO2_pH	Pro. micro.	Eco	S	M	S	Teira et al. (2012)

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Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
Le	Warming	Microinverts	Eco	M	M	M	Thompson and Shurin (2012)
Le	Salinity	Microinverts	Eco	M	M	M	
Le	Habitat change	Microinverts	Eco	M	M	M	
M	Warming	Microinverts	Comm	M	M	S	Thyssen et al. (2011)
M	Light	Microinverts	Comm	M	M	S	
T	Warming	Peren. plants	Eco	M	S	L	Tingey et al. (2007a)
T	CO2_fert	Peren. plants	Eco	M	S	L	
T	Warming	Peren. plants	Eco	M	S	L	Tingey et al. (2007b)
T	CO2_fert	Peren. plants	Eco	M	S	L	
M	Warming	Corals	Pop	S	S	M	Torrents et al. (2008)
T	Warming	Peren. plants	Pop	L	S	S	Turnbull et al. (2002)
Le	Warming	Peren. plants	Eco	M	S	L	Updegraff et al. (2001)
Le	Precipitation	Peren. plants	Eco	M	S	L	
Le	Diversity	Peren. plants	Eco	M	S	L	
T	Warming	Inverts	Comm	S	M	M	Uvarov et al. (2009)
T	Diversity	Inverts	Comm	S	M	M	
Le	CO2_fert	Peren. plants	Eco	S	S	M	Vann and Megonigal (2003)
Le	Precipitation	Peren. plants	Eco	S	S	M	
Le	Diversity	Peren. plants	Eco	S	S	M	
Le	Warming	Microinverts	Pop	M	M	L	Van Doorslaer et al. (2007)
Le	Warming	Macroinverts	Pop	M	M	L	Van Doorslaer et al. (2009)
Le	Warming	Macroinverts	Pop	M	M	L	Van Doorslaer et al. (2010)
M	Warming	Microinverts	Comm	S	S	S	Vázquez-Domínguez et al. (2012)

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	Warming	Seas. plants	Eco	M	M	L	Verburg et al. (2005)
T	Nutrients	Seas. plants	Eco	M	M	L	
T	Nutrients	Seas. plants	Eco	M	M	L	Veraart et al. (2011)
M	Warming	Peren. plants	Eco	S	S	S	
M	Light	Microinverts	Comm	M	M	S	
M	Warming	Microinverts	Comm	M	M	S	
M	Nutrients	Macroinverts	Pop	–	M	M	Vilchis et al. (2005)
M	Warming	Macroinverts	Pop	–	M	M	
M	CO2_pH	Microinverts	Eco	L	M	S	Vogt et al. (2008)
Le	Warming	Pro. micro.	Eco	S	L	L	Wang et al. (2012)
Le	Warming	Peren. plants	Comm	M	S	L	Weltzin et al. (2003)
Le	Precipitation	Peren. plants	Comm	M	S	L	
Le	Diversity	Peren. plants	Eco	M	S	L	White et al. (2008)
Le	Precipitation	Peren. plants	Eco	M	S	L	
Le	Warming	Peren. plants	Eco	M	S	L	
M	CO2_pH	Macroinverts	Eco	S	S	M	Widdicombe et al. (2009)
Le	Warming	Microinverts	Comm	S	S	S	Williamson et al. (2010)
Le	Light	Microinverts	Comm	S	S	S	
M	CO2_pH	Microinverts	Eco	L	M	S	Wingenter et al. (2007)
M	Warming	Microinverts	Eco	M	M	S	Wohlers-Zöllner et al. (2009)
M	Warming	Eu. micro.	Eco	S	M	M	Wohlers-Zöllner et al. (2011)
M	Nutrients	Eu. micro.	Eco	S	M	M	
Lo	Precipitation	Macroinverts	Comm	M	M	L	Woodward et al. (2012)
T	Warming	Pro. micro.	Comm	S	L	M	Wu et al. (2002)

Continued

Sys.	Driver	Focal taxon	Biological complexity	Vol.	Time (abs.)	Time (rel.)	References
T	Warming	Seas. plants	Eco	S	M	L	Wu et al. (2012)
T	Precipitation	Seas. plants	Eco	S	M	L	
T	Warming	Pro. micro.	Comm	S	L	M	Yergeau and Kowalchuk (2008)
T	Habitat change	Pro. micro.	Comm	S	L	M	
T	Precipitation	Macroinverts	Comm	S	S	M	Yli-Olli and Huhta (2000)
Le	Warming	Peren. plants	Eco	M	S	L	Yvon-Durocher et al. (2010a)
Le	Warming	Pro. micro	Eco	M	S	L	Yvon-Durocher et al. (2011a)
Le	Warming	Microinverts	Comm	M	S	L	Yvon-Durocher et al. (2011b)
Le	Warming	Pro. micro.	Eco	S	L	L	ZhiJian et al. (2012)

APPENDIX 6. LIST OF PAPERS USED TO CONSTRUCT THE DATABASE

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