

Improving the predictive power and interdisciplinarity of climate change experiments

Francois Rineau 1*, Robert Malina 2, Natalie Beenaerts 1, Natascha Arnauts 1, Richard D. Bardgett 3, Matty P. Berg 4,5, Annelies Boerema 6, Liesbeth Bruckers 7, Jan Clerinx 1, Edouard L. Davin 8, Hans J De Boeck 9, Tom De Dobbelaer 10, Marta Dondini 11, Frederik De Laender 12, Jacintha Ellers 4, Oscar Franken 4, Lucy Gilbert 13, Lukas Gudmundsson 8, Ivan A. Janssens 9, David Johnson 3, Sebastien Lizin 2, Bernard Longdoz 14, Patrick Meire 6, Dominique Meremans 6, Ann Milbau 10, Michele Moretti 2,15, Ivan Nijs 9, Anne Nobel 2, Sorin Pop 16, Thomas Puetz 17, Wouter Reyns 1,12, Jacques Roy 18, Jochen Schuetz 16, Sonia I. Seneviratne 8, Pete Smith 11, Francesca Solmi 7, Jan Staes 6, Wim Thiery 8,19, **Sofie Thijs 1**, Inne Vanderkelen 19, Wouter Van Landuyt 10, Erik Verbruggen 9, Nele Witters 2, Jakob Zscheischler 8,20,21, Jaco Vangronsveld 1, 22

* Corresponding author: Francois Rineau, Environmental Biology, Centre for Environmental Sciences, Hasselt University, Diepenbeek, Belgium. Email: francois.rineau@uhasselt.be

1 Hasselt University, Environmental Biology, Centre for Environmental Sciences, Agoralaan Gebouw D, 3590 Diepenbeek, Belgium

2 Hasselt University, Environmental Economics, Centre for Environmental Sciences, Agoralaan Gebouw D, 3590 Diepenbeek, Belgium

3 The University of Manchester, School of Earth and Environmental Sciences, Michael Smith Building, Manchester M13 9PT, UK

4 Vrije Universiteit Amsterdam, Department of Ecological Science, De Boelelaan 1085, 1081HV Amsterdam, The Netherlands

5 Groningen University, Groningen Institute for Evolutionary Life Science, Community and Conservation Ecology Group, Nijenborgh 7, 9747AG Groningen, The Netherlands

6 University of Antwerp, Ecosystem Management research group (ECOBIE), Universiteitsplein 1C, 2610 Antwerp, Belgium

27 7 Hasselt University, Interuniversity Institute for Biostatistics and Statistical Bioinformatics, Agoralaan
 28 Gebouw D, 3590 Diepenbeek, Belgium

29 8 ETH Zurich, Institute for Atmospheric and Climate Science, Universitaetstrasse 16, 8092 Zurich,
 30 Switzerland

31 9 University of Antwerp, Plants and ecosystems (PLECO), Universiteitsplein 1, 2610 Wilrijk, Belgium

32 10 Research Institute for Nature and Forest (INBO), Herman Teirlinckgebouw, Havenlaan 88 box 73,
 33 B-1000 Brussels, Belgium

34 11 University of Aberdeen, Institute of Biological and Environmental Sciences, 23 St Machar Drive,
 35 Aberdeen, AB24 3UU, UK

36 12 Namur University, Namur Institute of Complex Systems, and the Institute of Life, Earth, and
 37 Environment, Research Unit in Environmental and Evolutionary Biology, Rempart de la Vierge 8,
 38 5000 Namur , Belgium

39 13 University of Glasgow, Institute of Biodiversity, Animal Health and Comparative Medicine, Graham
 40 Kerr Building, G12 8QQ, UK.

41 14 University of Liege, Gembloux Agrobio Tech, TERRA, Res Ctr Atmosphere Ecosyst Exchanges, B-
 42 5030 Gembloux, Belgium

43 15 University of Liege, Gembloux Agrobio Tech, Department of Agricultural Economics and Rural
 44 Development, B-5030 Gembloux, Belgium

45 16 Hasselt University, Faculty of sciences, Agoralaan Gebouw D, 3590 Diepenbeek, Belgium

46 17 Forschungszentrum Juelich, Inst Bio & Geosci IBG-3: Agrosphere, Juelich, Germany

47 18 Ecotron Européen de Montpellier, Centre National de la Recherche Scientifique, 34980
 48 Montferrier-sur-Lez, France

49 19 Vrije Universiteit Brussel, Department of Hydrology and Hydraulic Engineering, Pleinlaan 2, 1050
 50 Brussels, Belgium

51 20 University of Bern, Climate and Environmental Physics, Sidlerstrasse 5, 3012 Bern, Switzerland

52 21 University of Bern, Oeschger Centre for Climate Change Research, Switzerland

22 Department of Plant Physiology, Faculty of Biology and Biotechnology, Maria Curie-Skłodowska
University, Lublin, Poland

55

56 Preface (100 words)

57 While the general *direction* of ecosystems' responses to a variety of climate change scenarios has
58 been well investigated, insights in the potential *amplitude* and *dynamics* of this response are scarce
59 and the societal impacts often remain unquantified. Drawing on the expertise of researchers from a
60 variety of disciplines, this paper outlines how methodological and technological advancements can
61 help design climate experiments that better capture the dynamics and amplitude of ecosystem
62 responses provoked by climate change and translate these responses into societal impacts.

63

64 1. Introduction

65 Climate change is expected to impact ecosystem communities and ecosystem functioning¹. Crop
66 yields², carbon (C) sequestration in soil³, and pollination rate⁴ are generally predicted to decrease,
67 while land evapotranspiration⁵ and tree mortality, especially in the Boreal region, are expected to
68 increase⁶. At the same time, the redistribution of species will increase opportunities for pest and
69 pathogen emergence¹.

70 These functions are crucial for human well-being through their contribution to ecosystem services,
71 and so impacting them will have important consequences for society⁷. However, refining the societal
72 cost estimations remains a challenge, partly because large knowledge gaps regarding the amplitude
73 and dynamics of these responses that make it difficult to plan for climate adaptation. Specifically
74 designed climate change experiments are necessary to address these issues. The goal of this
75 perspective paper is fourfold. First, while acknowledging the great advances achieved by climate
76 change-ecosystem responses experiments so far, we also identify the challenges that many of them
77 currently face: high complexity of climate change in terms of environmental variables, constraints in
78 the number and amplitude of climate treatment levels, and the limited scope with regard to

responses and interactions covered (Section 2). Second, to overcome these challenges we propose an experimental design that can leverage the increased computational and technological capabilities to more accurately capture the complexity of climate change in experiments; increase the number and range of climate treatment levels, and employ an interdisciplinary approach to broaden the range of responses and interactions covered (Section 3). Third, we outline an experiment that applies these design recommendations to demonstrate how it can enhance our capacity to understand and predict ecosystem responses to climate change. We describe the technical infrastructure used in this experiment, the climate manipulations, and the analysis pathway all the way to the valuation of the changes in ecosystem services (Section 4). Fourth, we place this design within the larger context of climate change experiments and pinpoint its complementarity to other designs (Section 5).

2. Challenges of climate change experiments

The complexity of climate change

The first challenge for research on climate change-ecosystem responses lies in the complex manner in which global climate change will affect local weather. To mimic a future climate, factors such as air temperature, atmospheric CO₂, and precipitation need to be manipulated in combination, which can be both conceptually and technologically challenging⁸. Therefore, a significant proportion of climate change experiments have focused on measuring the effects of specific combinations of climate factors (such as warming plus drought), manipulated using technology that was available or affordable at that time (such as passive night-time warming and rain exclusion curtains)⁹. Although these experiments have led to many invaluable outcomes, such approaches cannot fully cover the complexity of climate projections or the covariance of meteorological variables. As such, they may, for example, under- or overestimate the effects on ecosystem functioning of changes in the frequencies of frosts and heat waves, drought-heat-wave reinforcements¹⁰, interactions between soil moisture conditions and subsequent precipitation occurrence¹¹, increased frequencies of mild droughts (including in spring and autumn), and increased frequency of heavy precipitation events¹².

105 These climate alterations can have a strong influence on ecosystem functioning: for example,
106 decreased frost frequency may have a significant impact on plant mortality¹³ and more frequent mild
107 droughts can trigger plant acclimation and hence resistance to drought stress¹⁴. Therefore, many
108 climate change experiments did not simulate (i) an extreme event instead of a change in the mean
109 for a given single factor, (ii) regimes of events instead of a single event for a given single factor, and
110 (iii) complex coupling between multiple factors. This lack of refinement in climate manipulations
111 likely compromised the reliability of the estimation of ecosystem responses. Some steps have already
112 been taken to address this, by applying treatments of precipitation regime or heatwaves as observed
113 in the field^{15,16} and by using translocation experiments, where macrocosms are displaced across
114 geographic gradients in order to expose them to other climates that match possible future conditions
115 at the location of origin (space for time approach)¹⁷. However, such an issue cannot be solved by
116 modelling alone, because it requires testing too many possible interactions between factors, as well
117 as changing regimes of single factors.

118 *Climate treatment levels: number and range*

120 Because of the cost of specialized infrastructure, scientists are often limited in the number of
121 experimental units they can set up within a given experiment. Hence, climate factors are often
122 applied at only two levels: ambient and future projections⁹. This provides useful estimations on the
123 direction of ecosystem responses but does not provide insights into the shape of the responses to
124 these factors or how far away current conditions are from potential tipping points to alternative
125 stable states¹⁸. Moreover, ecosystem responses to multifactor global change drivers are regulated by
126 complex, nonlinear processes¹⁹, which makes modeling difficult with experimental data that comes
127 only from the two-level manipulation of environmental factors²⁰.

128 Also stemming from high equipment costs is the narrow range of climate treatments. Most
129 experiments have kept this range within conservative boundaries²¹, presumably because more
130 drastic (though realistic) climate treatments may have a catastrophic impact on a studied ecosystem,

131 potentially leading to the loss of expensively equipped replicates. The truncation of more extreme
132 climate conditions has, in turn, led to a lack of evidence regarding their effects on ecosystem
133 functioning.

134 Finally, low temporal resolution is also an issue. Because it requires an extensive and high frequency
135 monitoring of ecosystem functions, a substantial proportion of climate change experiments have
136 only measured the ecosystem dynamics or trajectories annually or seasonally. Such experiments may
137 fail to detect short-term dynamics of ecosystem responses²² or trajectories leading to a transition to
138 an alternative stable state^{23,24}. However, trends related to ecosystem dynamics often appear on
139 decadal time scales, because of the time needed to alter biogeochemical cycles and the properties of
140 soil organic matter. Therefore the duration of the monitoring should be prioritized over its frequency
141 if the setup does not allow a good coverage of both.

143 *Integration among disciplines*

144 The very nature of climate change and its impacts is discipline-spanning and therefore requires an
145 integrated approach²⁵. Although the number of interdisciplinary studies related to climate change is
146 increasing steadily²⁶, there are still many challenges related to interdisciplinary research. These
147 include establishing common terminology, concepts and metrics^{25,27,28}, a consistently lower funding
148 success for interdisciplinary research projects²⁹, and a general lack of interdisciplinary research
149 positions²⁵. The barriers depend largely on the purpose, forms and extent of knowledge integration,
150 and their combination³⁰. Although climate change research developed from multidisciplinarity to
151 interdisciplinarity, and further to transdisciplinarity³¹, most collaborative work in environmental
152 research is small-scale rather than large-scale interdisciplinary work³⁰. Small-scale integration refers
153 to collaborations between similar partners (for example, different natural science disciplines), while
154 large-scale integration crosses broader boundaries (such as between natural and social science)³⁰.
155 Currently, ecosystem services studies are mostly limited to either the natural science aspects or the
156 socio-economic science aspects and rarely cover the entire ecosystem services cascade³². This lack of

large-scale knowledge integration results in errors along this cascade; both when moving from biodiversity and ecosystem functions to ecosystem services, and when moving from ecosystem services to societal values.

3. Recommendations

Using climate model outputs and technology to refine climate change treatments

A first option to prescribe a projected change in weather dynamics is to alter specific characteristics (such as drought duration, heat wave intensity) in isolation using high-frequency data of ambient weather conditions so that they match future projections. The advantage of this method is that atmospheric conditions can be modified with high-quality field data instead of relying upon less precise regional climate model outputs with lower spatial and temporal resolution. Moreover, if used to manipulate one climate factor at a time, such an approach facilitates a mechanistic understanding of ecosystem responses that can be further extrapolated through modeling. This design may combine two or more factors to provide information about interactions between climate parameters.

Incorporating the complexity of projected changes can also be achieved by using outputs of state-of-the-art climate models. Due to model biases, the appropriate model must be selected very carefully. Global climate models (GCMs) are useful tools for assessing climate variability and change on global to continental scales, typically with a spatial resolution of 100–250 km. To estimate climate variability at more local scales, GCMs are dynamically downscaled using regional climate models (RCMs), which resolve the climate at higher resolutions (typically 10–50 km). The GCM/RCM combinations can then be chosen based on (i) how well models perform against local climate and weather characteristics in the studied ecosystem and (ii) how representative future projections are to the multi-model mean. In this case, one can simulate an ecosystem response to a given climate setup with higher accuracy. However, unlike with a full factorial experiment, it is not possible to attribute an ecosystem response to a given climate factor. Nevertheless, the model-output approach does facilitate the application of

increasingly high warming levels by using a global mean temperature gradient (see Section 4). It also addresses the issues of covarying variables, and it can be directly linked with a scenario from the Intergovernmental Panel on Climate Change which would represent a major step towards bridging the gap between climate and ecosystem science.

However, to implement these options it is necessary to control climate conditions and atmospheric composition with high frequency and high accuracy. This can be achieved only with dedicated and advanced equipment. Ecotron infrastructures, which consist of a set of replicated experimental units where environmental conditions are tightly controlled and where multiple ecosystem processes are automatically monitored, are well-suited to fulfill these needs³³. Such infrastructures have been historically limited to a handful across the world⁹, but are becoming increasingly widespread^{34–36}. They also offer the opportunity to monitor ecosystem responses at sub-hourly frequencies, making it possible to simultaneously discriminate between short- and long-term ecosystem responses.

Increasing the number and range of climate treatment levels

A gradient design, in which one or several climate factors are applied at increasingly high levels, can substantially increase the resolution of a climate change experiment. This is better suited to quantitatively describing the relationship between a response variable and a continuous climate factor than the more traditional approach of testing ambient versus a single future projection, and allows the collection of quantitative data for ecological models³⁷. It also makes it possible to detect nonlinearity, thresholds, and tipping points, and to interpolate and extrapolate ecosystem responses¹⁸. While such gradient designs should ideally be replicated, unreplicated regression designs can be a statistically powerful way of detecting response patterns to continuous and interacting environmental drivers, provided that the number of levels in the gradient is large enough³⁷.

To ensure appraisal of the largest possible range of ecosystem responses, the gradient should be as long as possible, even extending beyond the most extreme conditions. Broader treatment modalities can also inform how far a specific ecosystem response is situated relative to its upper or lower tolerance limit. In addition, the levels of the gradient may be spread in a non-linear manner to achieve the highest resolution in the range where the strongest ecosystem responses are expected.

Employing an interdisciplinary approach to better capture responses and interactions

We argue that an overarching objective of climate change experiments is to contribute to the understanding of the impacts that climate change has on nature and society as well as to enlarge our potential for climate adaptation. However, as outlined in Section 2, the lack of large-scale knowledge integration can result in errors along the ecosystem services cascade; first in the step from biodiversity and ecosystem functions to ecosystem services and second from ecosystem services to societal values.

Regarding the first step, thorough quantification of ecosystem services should be based on specific data regarding how the ecosystem is functioning. Many ecosystem service studies use land use as an indicator of ecosystem service delivery³², but often land use classification cannot capture differences between abiotic conditions and ecological processes that explain differences in service delivery³⁸. Therefore, using land use as a simple indicator will result in inappropriate management decisions³⁸.

Regarding the second step, economists need to be involved early in the process. Although there are many ways in which ecosystem function changes can affect the provision of ecosystem services to society³⁹. However, budget constraints necessitate the selection of those ecosystem functions and services that are considered most important to society. A common selection approach is to consider the potential impact of ecosystem changes in terms of human welfare endpoints, often by means of monetary valuation. Ecologists and economists must interact across disciplinary boundaries if ecological experiments are intended to predict these endpoints within an ecosystem services context⁴⁰. Hence, economists need to be involved during the design of ecological experiments in

order to ensure that those ecosystem service changes that are most relevant for human welfare are measured and predicted.

We suggest that, the desired large-scale integration can be achieved in several steps, organized in a top-down approach. The first step is to identify the key ecosystem services to value based on welfare endpoints⁴¹. For most terrestrial ecosystems, this would imply assessing services from the following list: food and raw material production and quality, water supply and quality, C sequestration, depollution, erosion prevention, soil fertility, pest and pathogen control, pollination, maintenance of biodiversity and recreation. The second step consists of identifying the set of variables that best describes the ecosystem functions, processes and structures associated with these services. Based on the literature⁴², we suggest the following measures (see also Table 1): (i) vegetation variables (plant community structure, above/belowground biomass, litter quality), (ii) atmospheric parameters (net ecosystem exchange, greenhouse gas emissions), (iii) soil abiotic (pH, texture, electrical conductivity, macro-, micronutrient and pollutant content) and biotic (fauna and microbial community structure, respiration, and biomass) variables, and (iv) all parameters that describe movements of water in the soil-plant-atmosphere continuum (precipitation, leaching, air relative humidity, evapotranspiration, water potential). Air and soil temperatures should also be monitored, since they determine biogeochemical reaction rates. Finally, ecosystem processes, structures and functions need to be translated into services, and ultimately into societal value by expressing them in monetary and non-monetary terms. Measuring all of these variables, integrating them in an ecosystem service framework, and estimating the societal value of these services would require expertise from plant ecologists and ecophysiologists, hydrologists, soil biogeochemists, animal ecologists, microbiologists, pedologists, climatologists, as well as modelers and environmental economists⁴³.

4. An initial application of the recommendations: The UHasselt Ecotron experiment

Here we describe our proposed interdisciplinary approach in the context of a climate change manipulation using the UHasselt Ecotron experiment.

Ecotron infrastructure

The UHasselt Ecotron facility consists of tightly controlled climate change manipulations of 12 macrocosms (soil-canopy columns of 2 m in diameter and 1.5 m depth), extracted without significant disruption of the soil structure from a dry heathland plot in the 'Hoge Kempen' National Park (50° 59' 02.1" N, 5° 37' 40.0" E) in November 2016. The plot was managed for restoration six years before the sampling. The design of this infrastructure benefited from exchanges through the AnaEE (Analysis and Experimentation on Ecosystems)/ESFRI (European Strategy Forum on Research Infrastructure) project. Some of the infrastructure's features were inspired by the Macrocosms platform of the CNRS Montpellier Ecotron¹⁶. Each UHasselt Ecotron unit consists of three compartments: the dome, the lysimeter, and the chamber. The dome consists of a shell-shaped dome made of highly PAR (photosynthetically active radiation) transparent material, where wind and precipitation are generated and measured and where the concentration of greenhouse gases (CO₂, N₂O, CH₄), PPFD (photosynthetic photon flux density) and difference between incoming and outgoing short- and long-wave radiation are measured. The lysimeter (equipment for measuring hydrological variations undergone by a body of soil under controlled conditions) contains the soil-canopy column, where soil-related parameters are controlled (including the vertical gradient of soil temperature and water tension) and measured, and is weighed every minute. Suction cups and soil sensors are installed following a triplicated 5 depth design (Fig. S1). The chamber is a gastight room that encloses the lysimeter, where air pressure, air temperature, relative humidity, and CO₂ concentration are controlled and key variables measured in each unit (Fig. S1). The UHasselt Ecotron is linked with a nearby Integrated Carbon Observation System (ICOS) ecosystem tower (<https://www.icos-ri.eu/home>), which provides real-time data on local weather and soil conditions, with a frequency of at least 30 minutes.

Climate manipulations

A double-gradient approach is adopted: one approach (six units) measures the effect of an altered single factor (here, precipitation regime), while maintaining the natural variation of other abiotic factors, and the other approach (six units) manipulates climate by jointly simulating all covarying parameters, representing increasingly intense climate change. The two approaches are described below. Because they sit isolated in an enclosed facility, it is possible that small initial differences in the soil-canopy core in a given unit will increase with time to the point where it becomes statistically different from the others. Therefore, the units were first distributed within the two gradients using a cluster analysis to minimize the noise in ecosystem responses measured during a test period (see Fig. S2) due to small-scale soil heterogeneity. This clustering was used to distribute the units according to the pattern shown in Fig. 1.

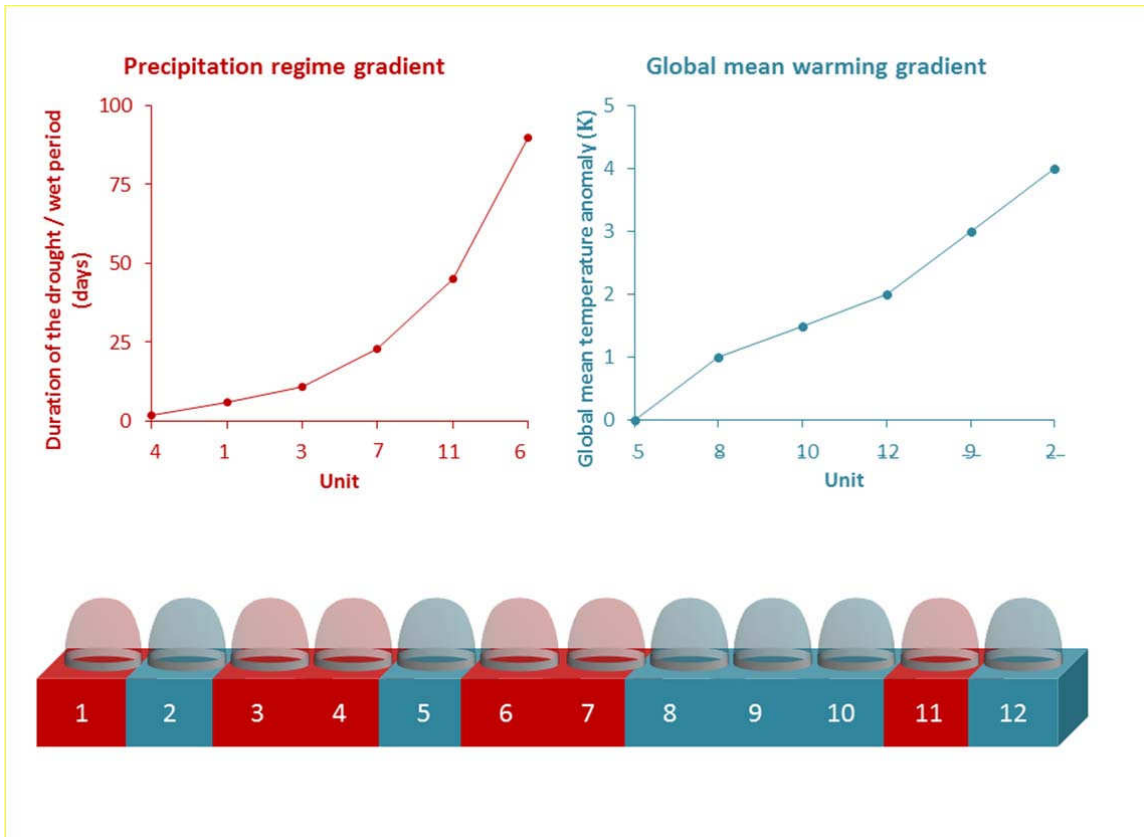


Figure 1. Overview of the two climate change gradient designs in the UHasselt Ecotron experiment. The units have been redistributed to maximize statistical similarity within a gradient prior to the

treatment. Global mean temperature anomalies are computed with respect to the reference period 1951-1955.

Climate change projections for the NW Europe region predict higher probability of both heavier precipitation and longer droughts, without a significant change in yearly precipitation⁴⁴. The precipitation regime gradient uses real-time input from the ecosystem tower nearby, and only alters precipitation events: across the gradient, increasingly long periods (2, 6, 11, 23, 45 and 90 days), based on local climate records from Maastricht, NL⁴⁵) in which precipitation is withheld (dry period) are followed by increasingly long periods in which precipitation is increased (wet period), with the duration of the two periods kept equal within a unit (Fig. 1). Precipitation events during the wet period are increased twofold and are adjusted at the end of the period to avoid altering the yearly precipitation amount.

To drive the second gradient of the UHasselt Ecotron experiment, we use the climate variables produced by an RCM following Representative Concentration Pathway (RCP) 8.5, a high-emission scenario⁴⁶. The gradient itself is determined based on global mean temperature anomalies. In the six units, climates corresponding to a +0 ° to +4 °C warmer world (projected for periods ranging from 1951–1955 to 2080–2089) are simulated (Fig. 1, Fig. S3), by extracting local climate conditions from the RCM for periods consistent with these warming levels (Fig. S3)⁴⁷. This set-up also facilitates comparison of the ‘present-day’ climate as simulated by the RCM (the +1 °C unit), to the unit driven by ICOS field observations. Moreover, the climate simulated in the +1.5° C unit is reasonably consistent with the lower end of the long-term temperature goals set by the Paris Agreement⁴⁸.

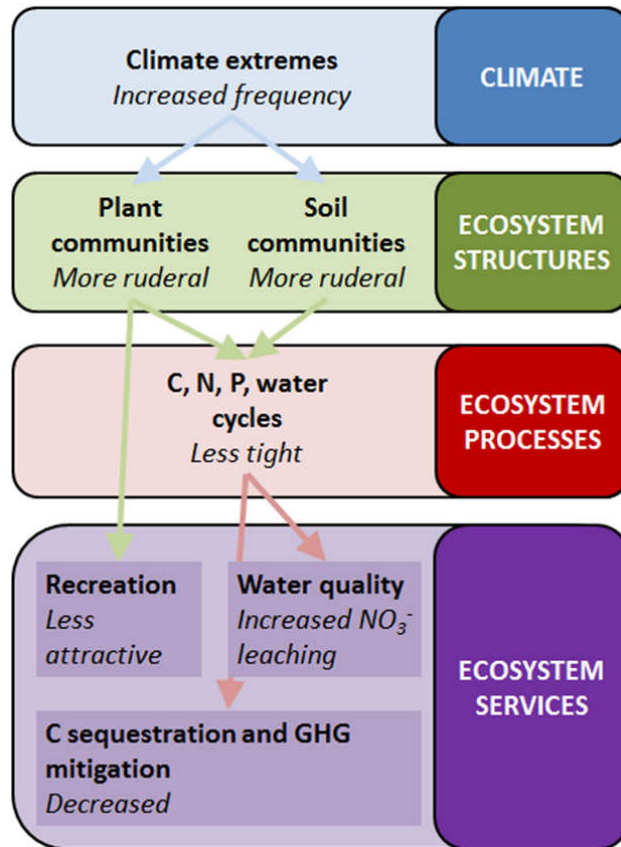


Figure 2. Impact pathway showing the reasoning behind the integration of scientific disciplines in the UHasselt Ecotron experiment. The research hypotheses are given in italics and described in more detail in Fig. S4.

Integrating scientific disciplines for an interdisciplinary ecosystem service approach

As outlined in Section 3, climate change experiments require large-scale knowledge integration to enable more useful estimates of climate change effects on ecosystem functioning and on society. The UHasselt Ecotron facility makes it possible to extend the degree of interdisciplinarity by investigating the entire cascade from climate changes to ecosystem functions, ecosystem services, and, finally, societal values. As such, the ecotron facility contributes to the development towards large-scale knowledge integration on climate change. Consequently, the UHasselt Ecotron experiment brings together several disciplines in an interdisciplinary framework (Fig 2). With input from other involved

disciplines, climatologists design the protocols for climate manipulations and plant ecologists monitor plant communities in each ecotron unit. Numerical models for water movement within one unit are developed by mathematicians and hydrologists. Ecotron output on C cycling is fed into a soil C model⁴⁹, both for calibration and prediction purposes. Community modelers improve the power of this model by accounting for the soil community structure and species interactions (food web). The specific role of soil organisms in soil biogeochemistry is investigated by microbial and soil fauna ecologists. This is inferred from variation in responses of different functional groups such as nitrogen fixers, mycorrhizal fungi and different feeding guilds of soil fauna, combined with additional separate experiments, both in the field and *in vitro*. The outputs of the measurements above (see Table 1) allow experts in ecosystem ecology to quantify ecosystem services. Environmental economists express the change in ecosystem services provided using best-practice monetization approaches⁵⁰. For example, water quality regulation is assessed as the prevented cost of intensified water treatment or use of other water resources. Measurements of vegetation, soil abiotic parameters and the water balance make it possible to quantify this benefit. Carbon sequestration is assessed as the prevented cost from increased global temperature, which can be quantified based on vegetation, air parameters and soil abiotic parameters measurements. Maintenance of biodiversity and recreation can be assessed based on measurements of vegetation.

We note that (monetary) estimates from an individual study can often not be applied directly for generating policy-recommendations⁵¹, especially for complex and spatially heterogeneous problems such as climate change impacts on ecosystems. However, meta-analyses need to rely on data generated by primary studies that estimate the societal cost (or benefit) of changes in specific services provided by a specific ecosystem at specific location(s). In this regard, the UHasselt Ecotron experiment can also provide valuable input data for dedicated policy-guiding analyses⁵².

Table 1. Measured variables in the UHasselt Ecotron experiment and links with ecosystem functions, services, and values. Left-hand side of the table: ecosystem services. Right-hand side: variables measured in the ecotron experiment. Lower part of the table: illustration of how the societal value of four of the ecosystems services will be assessed.

ECOSYSTEM SERVICES											MEASURED VARIABLES			
Food	Raw materials	Water quality	C sequestration	Erosion prevention	Maintenance of biodiversity	Recreation	Climate regulation	Water retention	Soil fertility	Depollution	Pathogen control	Variable category	Variable	Frequency of measurement
o	o	o	o	o	o	o						Vegetation	Plant community structure	6 months
o	o	o	o	o	o								Shoot & root biomass	6 months
			o									Air parameters	Net ecosystem exchange (NEE)	30 min
			o				o						Temperature	2 min
													GHG emissions (CH4, N2O)	2 min
				o					o	o		Soil abiotic parameters	Texture	1 year
			o					o	o				Temperature	2 min
										o			Biochemical composition	1 year
		o							o				Electrical conductivity	30 min
		o								o			Soil pore water chemistry	2 weeks
											o		Available pollutant concentration	1 year
											o	Soil biotic parameters	Fauna community structure	6 months
				o							o		Microbial community structure	6 months
											o		Mineralization rate	1 year
		o		o				o				Water balance	Precipitation	30 min
		o						o	o	o			Leaching	30 min
		o						o					Relative humidity	30 min
		o						o					Evapotranspiration	30 min
		o						o					Soil water potential	30 min
ECONOMIC VALUATION														
													Prevented cost of intensified water treatment or use of other water resources	
													Prevented damage cost from increased global temperature	
													Non-use value of continued existence of biodiversity	
													Use value of recreational enjoyment	

5. The place of the suggested design within the landscape of climate change experiments

A comprehensive understanding of ecosystem responses to climate change can only be achieved through the use of a broad range of different, complementary experimental designs, all of which can be integrated through modeling. The experimental design suggested here exhibits a unique set of advantages and drawbacks, which makes it suited to tackle specific needs within the climate change experiments landscape.

Strengths and limitations of the design

The strengths of the suggested design comprises (1) high-performance microclimate conditioning, both above- and belowground, which makes it possible to approximate field conditions while maintaining control, (2) high-frequency automated measurements of ecosystem functions and thus

of treatment impact thereon, and (3) a large-scale interdisciplinary approach. The first two strengths are inherent to the ecotron research infrastructure, while the large-scale integration can theoretically be implemented in any climate change experiment. However, we consider ecotron infrastructures to be particularly suitable for such an interdisciplinary approach, because of the high-end climate control and the broad range of functions monitored at a high frequency.

With respect to (1), studies focusing on ecosystem functions, processes and structures that are highly sensitive to soil temperature and soil water potential would benefit most from being conducted in ecotrons (for example, soil CO₂ exchange and C sequestration, growth and activity of soil microbes and soil fauna), as the lysimeter component can generate very precise lower boundary conditions and thus realistic vertical soil profiles of temperature and soil water status. With respect to (2), studies in which the high-resolution temporal pattern of ecosystem functions and their coupling is important would also benefit from ecotron infrastructures, as it is difficult to measure these parameters manually across long time scales. For example, simultaneous automated measurement of the carbon, water and mineral nutrient cycles makes it possible to disentangle their interactions in a range of climate conditions, and to feed control mechanisms into models.

A first set of constraints in the usefulness of the experimental design described in this paper stems from the scale limitation of the experimental units. Ecotrons can accommodate plants only of small stature (less than two meters in height), which excludes forests and tall crops. For the same reason, the impact of megafauna such as grazers or top predators cannot be tested. Results obtained in macrocosms only integrate small-scale (less than one meter) variability, which leads to a lack of accuracy when scaling up to ecosystem.

Second, it may be difficult to financially support this type of experiment on the time scale of ecosystem responses (10 years or more)⁵³. Ecosystem shifts to alternative stable states may remain undetected if the funding period is shorter than the period required for the ecosystem to shift. A partial solution for this would be to adopt a gradient design with increasingly late endpoints of

410 projected climate change; this would allow for some extrapolation of ecosystem response in time
411 (trajectories), which is possibly enough to estimate ranges of this response in the longer term.

412 Third, macrocosms in ecotron facilities are isolated from their ecosystem of origin. Hence genetic
413 input from propagules or pollination probably differ significantly from the field, which can be an
414 issue, especially in long-term experiments. This could be mitigated in two ways. The first is by
415 minimizing sampling disturbance, by sampling for soil microbes and soil fauna not more than twice a
416 year, using 10 cm diameter soil cores, this would account for only 1.5% of total soil surface annually.
417 The second way is by replacing soil sampling cores in the lysimeter by cores taken from the same
418 ecosystem. This would also avoid holes at the soil surface that may alter water flow through the soil
419 column. Furthermore, field traps to collect airborne propagules can be collected yearly and their
420 content spread on the enclosed surface of the soil-canopy columns. These solutions would at least
421 ensure fresh genetic input into the system, even though this input may be different in the field in
422 future conditions.

423 Finally, radiation in ecotron enclosures sometimes differ than in the field. Artificial LED-lightning
424 allows to control radiation precisely but is yet not able to reach the same radiation level as in the
425 field, while ambient lightning can disrupt its synchronization with temperature or precipitation. This
426 may be an issue while simulating heatwaves and droughts, which have more sunshine hours than
427 wet periods⁵⁴.

429 *Complementarity with other climate change experiments*

430 The weaknesses of the proposed design (small spatial scale, potentially insufficient time-scale, lack of
431 interaction with the surrounding environment) can be mitigated further through the use of
432 complementary experiments, which might even be partially integrated into the overarching
433 approach. For example, owing to small spatial scale, the results might have limited validity as a
434 predictor of ecosystem responses at other sites and in other habitats. Running experiments in
435 parallel across multiple climates and locations with the same methodology, also known as

“coordinated distributed experiments” (CDEs), would be better suited for this purpose as it allows extrapolation and generalization of results while correcting for effect size⁵⁵. For example, such a design makes it possible to study plant response to nutrient addition and herbivore exclusion⁵⁶; and ecological responses to global change factors across 20 eco-climate domains using a set of observatory sites⁵⁷. In fact, a coordinated distributed experiment using the design presented in Section 4, and testing the same climate gradient in different ecosystems across several ecotron facilities would combine the high generalization potential of CDEs with the precision of ecotrons.

A second area for potential complementarity and integration is translocation experiments. These experiments are well suited for long-term observations due to their relatively low funding requirements and relative ease of implementation, and the soil macrocosms used in these experiments are still connected to their surrounding environment¹⁷. However, the functioning of the ecosystem is monitored less comprehensively and frequently within these types of experiments and the influence of different climate factors on ecosystem functioning cannot be disentangled. Consequently, running an ecotron and a translocation experiment in parallel on the same ecosystem with similar climate treatments would make it possible to estimate the effect size of the connection with the surrounding environment on ecosystem response to climate change. This information can then, in turn, be used to correct the outputs of future ecotron experiments by accounting for the isolation factor.

Usefulness of the suggested design for modeling ecosystem response to climate change

While ecosystem models can be evaluated and calibrated using a range of data sources, including sites in different climate zones and long-term experiments without climate manipulation⁵⁸, data from well-controlled, replicated and highly instrumented facilities such as those described here are invaluable for testing the process understanding encapsulated in the models, and for testing model behavior against detailed, multi-parameter observations³⁶. Models that are tested and, where necessary, calibrated against such data can then be evaluated against data from other sites. If the

outputs do not prove to be generalizable, the information derived from testing the model could be used to refine the experimental design and explain variation in the measured values. If the outputs prove generalizable, the models can be used across larger temporal and spatial scales to project potential impacts of future climate change^{59,60}.

6. Conclusion

The effects of climate change on ecosystem functioning have far-reaching consequences for society. Here we present a type of experiment that is designed to estimate the amplitude and dynamics of ecosystem responses to climate change, and the consequences for ecosystem services. We have outlined that climate change experiments are facing three types of challenges: limitations in addressing the complexity of climate change in terms of control of environmental variables, constraints in the number and range of climate level treatments, and restrictions in scope. We have suggested ways to address these challenges: improving computational and technological capabilities, increasing the number and range of climate treatment levels, and employing an interdisciplinary approach. We illustrated these suggestions through a case study where they have been implemented, and outlined the place of this design in the broader landscape of climate change experiments.

We foresee that the holistic approach outlined in this perspective could yield more reliable, quantitative predictions of terrestrial ecosystem response to climate change, and could improve knowledge on the value of ecosystem services and their links with ecosystem processes. We expect these results to be of interest for society beyond just scientists: they provide nature managers with predictions on ecosystem responses to help them decide on ecosystem management practices in the mid- and long-term, and that they will explain to policymakers and the wider public the societal impact of ecosystem changes induced by climate change at a more detailed, ecosystem-specific level.

Acknowledgments

The authors thank the Flemish government (through Hercules Stichting big infrastructure and the Fund for Scientific Research Flanders project G0H4117N), LSM (Limburg Sterk Merk, project 271) for providing funds to build the UHasselt Ecotron; Hasselt University for both funding and policy support (project BOF12BR01 and Methusalem project 08M03VGRJ); and the ecotron research committee for useful comments on the experimental design. We also thank RLKM (Regional Landscape Kempen and Maasland) for its collaboration and support. Nele Witters, Sebastien Lizin, Anne Nobel, and Inne Vanderkelen are funded by Research Foundation-Flanders (FWO).

Authors' contributions

FR and RM took the lead in writing the manuscript and received input from all co-authors. The initial conceptualization of this manuscript was discussed during a consortium meeting. All authors proofread and provided their input to different draft versions and gave their final approval for submission.

References

1. Scheffers, B. R. *et al.* The broad footprint of climate change from genes to biomes to people. *Science* (80-.). **354**, (2016).
2. Zhao, C. *et al.* Temperature increase reduces global yields of major crops in four independent estimates. 1–6 (2017). doi:10.1073/pnas.1701762114
3. Allen, C. D. *et al.* A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* **259**, 660–684 (2010).
4. Hat, J. L. & Prueger, J. H. Temperature extremes : Effect on plant growth and development. **10**, 4–10 (2015).
5. Collins, M. *et al.* Long-term Climate Change: Projections, Commitments and Irreversibility. in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Stocker, T. F. et

- 514 al.) 1029–1136 (Cambridge University Press, Cambridge, United Kingdom and New York, NY,
515 USA, 2013). doi:10.1017/CBO9781107415324.024
- 516 6. Pecl, G. T. *et al.* Biodiversity redistribution under climate change: Impacts on ecosystems and
517 human well-being. **9214**, (2017).
- 518 7. Millenium Ecosystem Assessment. *Ecosystems and human well-being: Synthesis*. Island Press,
519 Washington, DC. (2005). doi:10.1196/annals.1439.003
- 520 8. Leuzinger, S. *et al.* Do global change experiments overestimate impacts on terrestrial
521 ecosystems? *Trends Ecol. Evol.* **26**, 236–241 (2011).
- 522 9. Stewart, R. I. A. *et al.* Mesocosm Experiments as a Tool for Ecological Climate-Change
523 Research. *Advances in Ecological Research* **48**, (Elsevier Ltd., 2013).
- 524 10. Zscheischler, J. & Seneviratne, S. I. Dependence of drivers affects risks associated with
525 compound events. *Sci. Adv.* **3**, 1–11 (2017).
- 526 11. Guillod, B. P., Orlowsky, B., Miralles, D. G., Teuling, A. J. & Seneviratne, S. I. Reconciling spatial
527 and temporal soil moisture effects on afternoon rainfall. *Nat. Commun.* **6**, 1–6 (2015).
- 528 12. Thiery, W. *et al.* Hazardous thunderstorm intensification over Lake Victoria. *Nat. Commun.* **7**,
529 1–7 (2016).
- 530 13. Berendse, F., Schmitz, M. & Visser, W. De. Experimental Manipulation of Succession in
531 Heathland Ecosystems. *Oecologia* **100**, 38–44 (1994).
- 532 14. Backhaus, S. *et al.* Recurrent Mild Drought Events Increase Resistance Toward Extreme
533 Drought Stress. *Ecosystems* **17**, 1068–1081 (2014).
- 534 15. Verburg, P. S. J. *et al.* Impacts of an anomalously warm year on soil nitrogen availability in
535 experimentally manipulated intact tallgrass prairie ecosystems. *Glob. Chang. Biol.* **15**, 888–
536 900 (2009).
- 537 16. Roy, J. *et al.* Elevated CO₂ maintains grassland net carbon uptake under a future heat and
538 drought extreme. *Proc. Natl. Acad. Sci.* **113**, 6224–6229 (2016).
- 539 17. Cantarel, A. M. & Bloor, J. M. G. Four years of simulated climate change reduces above-

- ground productivity and alters functional diversity in a grassland ecosystem. **24**, 113–126 (2013).
18. Kreyling, J. *et al.* To replicate, or not to replicate - that is the question: how to tackle nonlinear responses in ecological experiments. *Ecol. Lett.* (2018). doi:10.1111/ele.13134
 19. Zhou, X., Weng, E. & Luo, Y. Modeling patterns of nonlinearity in ecosystem responses to temperature, CO₂, and precipitation changes. *Ecol. Appl.* **18**, 453–466 (2008).
 20. Luo, Y. *et al.* Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Glob. Chang. Biol.* **14**, 1986–1999 (2008).
 21. Kayler, Z. E. *et al.* Experiments to confront the environmental extremes of climate change. (2015). doi:10.1890/140174
 22. Svenning, J. C. & Sandel, B. Disequilibrium vegetation dynamics under future climate change. *Am. J. Bot.* **100**, 1266–1286 (2013).
 23. Harris, R. M. B. *et al.* Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Chang.* **8**, 579–587 (2018).
 24. Scheffer, M., Carpenter, S., Foley, J. a, Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* **413**, 591–6 (2001).
 25. Hein, C. J. *et al.* Overcoming early career barriers to interdisciplinary climate change research. *Wiley Interdiscip. Rev. Clim. Chang.* **9**, 1–18 (2018).
 26. Xu, X., Goswami, S., Gullett, J., Wulfschleger, S. D. & Thornton, P. E. Interdisciplinary research in climate and energy sciences. *Wiley Interdiscip. Rev. Energy Environ.* **5**, 49–56 (2016).
 27. Sievanen, L., Campbell, L. M. & Leslie, H. M. Challenges to Interdisciplinary Research in Ecosystem-Based Management. *Conserv. Biol.* **26**, 315–323 (2012).
 28. Abiven, S. *et al.* Integrative research efforts at the boundary of biodiversity and global change research. *Curr. Opin. Environ. Sustain.* **29**, 215–222 (2017).

- 566 29. Bromham, L., Dinnage, R. & Hua, X. Interdisciplinary research has consistently lower funding
567 success. *Nature* **534**, 684–687 (2016).
- 568 30. Turner, L. M. *et al.* Transporting ideas between marine and social sciences: experiences from
569 interdisciplinary research programs. *Elem Sci Anth* **5**, (2017).
- 570 31. Hellsten, I. & Leydesdorff, L. The construction of interdisciplinarity: the development of the
571 knowledge base and programmatic focus of the journal Climatic Change, 1977-2013. *J. Assoc.*
572 *Inf. Sci. technology* **67**, 2181–2193 (2016).
- 573 32. Boerema, A., Rebelo, A. J., Bodi, M. B., Esler, K. J. & Meire, P. Are ecosystem services
574 adequately quantified? *J. Appl. Ecol.* **54**, 358–370 (2017).
- 575 33. Clobert, J. *et al.* How to Integrate Experimental Research Approaches in Ecological and
576 Environmental Studies : AnaEE France as an Example. **6**, (2018).
- 577 34. Mougin, C. *et al.* A coordinated set of ecosystem research platforms open to international
578 research in ecotoxicology, AnaEE-France. *Environ. Sci. Pollut. Res.* **22**, 16215–16228 (2015).
- 579 35. Eisenhauer, N. & Türke, M. From climate chambers to biodiversity chambers. *Front. Ecol.*
580 *Environ.* **16**, 136–137 (2018).
- 581 36. Milcu, A. *et al.* Functional diversity of leaf nitrogen concentrations drives grassland carbon
582 fluxes. *Ecol. Lett.* **17**, 435–444 (2014).
- 583 37. Cottingham, K. L., Lennon, J. T. & Brown, B. L. Knowing when to draw the line : designing more
584 informative ecological experiments. *Front. Ecol. Environ.* **3**, 145–152 (2005).
- 585 38. Van der Biest, K. *et al.* Evaluation of the accuracy of land-use based ecosystem service
586 assessments for different thematic resolutions. *J. Environ. Manage.* **156**, 41–51 (2015).
- 587 39. Polasky, S. & Segerson, K. Integrating Ecology and Economics in the Study of Ecosystem
588 Services: Some Lessons Learned. *Annu. Rev. Resour. Econ.* **1**, 409–434 (2009).
- 589 40. Inkpen, S. A. & Desroches, C. T. When Ecology Needs Economics and Economics Needs
590 Ecology: Interdisciplinary Exchange in the Age of Humans. **21** (2019).
- 591 41. Costanza, R. *et al.* Changes in the global value of ecosystem services. *Glob. Environ. Chang.* **26**,

592 152–158 (2014).

593 42. Braat, L. C. & de Groot, R. The ecosystem services agenda:bridging the worlds of natural
594 science and economics, conservation and development, and public and private policy. *Ecosyst.*
595 *Serv.* **1**, 4–15 (2012).

596 43. Plaas, E. *et al.* Towards valuation of biodiversity in agricultural soils: A case for earthworms.
597 *Ecol. Econ.* **159**, 291–300 (2019).

598 44. Brouwers, J. *et al.* *MIRA Climate Report 2015, about observed and future climate changes in*
599 *Flanders and Belgium.* (2015). doi:10.13140/RG.2.1.2055.8809

600 45. Klein Tank, A. M. G. *et al.* Daily dataset of 20th-century surface air temperature and
601 precipitation series for the European Climate Assessment. *Int. J. Climatol.* **22**, 1441–1453
602 (2002).

603 46. van Vuuren, D. P. *et al.* The representative concentration pathways: An overview. *Clim.*
604 *Change* **109**, 5–31 (2011).

605 47. Seneviratne, S. I., Donat, M. G., Pitman, A. J., Knutti, R. & Wilby, R. L. Allowable CO₂emissions
606 based on regional and impact-related climate targets. *Nature* **529**, 477–483 (2016).

607 48. UNFCCC. Conference of the Parties (COP). Paris Climate Change Conference-November 2015,
608 COP 21. *Adopt. Paris Agreement. Propos. by Pres.* **21932**, 32 (2015).

609 49. Smith, J. *et al.* Estimating changes in Scottish soil carbon stocks using ECOSSE. II. Application.
610 *Clim. Res.* **45**, 193–205 (2010).

611 50. Schaubroeck, T. *et al.* Environmental impact assessment and monetary ecosystem service
612 valuation of an ecosystem under different future environmental change and management
613 scenarios ; a case study of a Scots pine forest. *J. Environ. Manage.* **173**, 79–94 (2016).

614 51. Hunter, J. E. & Schmidt, F. L. Cumulative research knowledge and social policy formulation:
615 The Critical Role of Meta-Analysis. *Psychol. Public Policy, Law* **2**, 324–347 (1996).

616 52. Gerstner, K. *et al.* Will your paper be used in a meta-analysis? Make the reach of your
617 research broader and longer lasting. *Methods Ecol. Evol.* **8**, 777–784 (2017).

- 618 53. Knapp, A. K. *et al.* Past , Present , and Future Roles of Long-Term Experiments in the LTER
619 Network. **62**, 377–389 (2012).
- 620 54. De Boeck, H. ., Dreesen, F. E., Janssens, I. A. & Nijs, I. Climatic characteristics of heat waves
621 and their simulation in plant experiments. *Glob. Chang. Biol.* **16**, 1992–2000 (2010).
- 622 55. Fraser, L. H. *et al.* Coordinated distributed experiments : an emerging tool for testing global
623 hypotheses in ecology and environmental science. (2013). doi:10.1890/110279
- 624 56. Lind, E. M. *et al.* Life-history constraints in grassland plant species : a growth-defence trade-
625 off is the norm. 513–521 (2013). doi:10.1111/ele.12078
- 626 57. Keller, M., Schimel, D. S., Hargrove, W. W. & Hoffman, F. M. A continental strategy for the
627 National Ecological Observatory Network. *Front. Ecol. Enviornment* **6**, 282–284 (2008).
- 628 58. Smith, P. *et al.* Towards an integrated global framework to assess the impacts of land use and
629 management change on soil carbon : current capability and future vision. 2089–2101 (2012).
630 doi:10.1111/j.1365-2486.2012.02689.x
- 631 59. Richards, M. *et al.* High-resolution spatial modelling of greenhouse gas emissions from land-
632 use change to energy crops in the United Kingdom. **44**, 627–644 (2017).
- 633 60. Song, J. *et al.* A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling
634 responses to global change. *Nat. Ecol. Evol.* (2019). doi:10.1038/s41559-019-0958-3
635