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Towards more predictive and interdisciplinary climate change ecosystem experiments

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56 Preface

In spite of the great advances achieved so far, experiments about the response of ecosystems to climate change still face significant challenges, including the high complexity of climate change in terms of environmental variables, constraints in the number and amplitude of climate treatment levels, and the limited scope with regard to responses and interactions covered. Drawing on the expertise of researchers from a variety of disciplines, this Perspective outlines how computational and technological advancements can help design experiments that can contribute to overcoming these challenges and outlines a first application of such an experimental design.

64

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 article is fourfold. First, while acknowledging the great advances achieved by climate 76 change-ecosystem responses experiments so far, we 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

79 responses and interactions covered (Section 2). Second, to overcome these challenges we propose 80 an experimental design that can leverage the increased computational and technological capabilities 81 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 82 83 range of responses and interactions covered (Section 3). Third, we outline an experiment that applies 84 these design recommendations to demonstrate how it can enhance our capacity to understand and 85 predict ecosystem responses to climate change. We describe the technical infrastructure used in this 86 experiment, the climate manipulations, and the analysis pathway all the way to the valuation of the 87 changes in ecosystem services (Section 4). Fourth, this design is placed within the larger context of 88 climate change experiments and pinpoint its complementarity to other designs (Section 5).

89

90 2. Challenges of climate change experiments

91 Climate change experiments are facing three types of challenges: limitations in addressing the
92 complexity of climate change in terms of control of environmental variables, constraints in the
93 number and range of climate level treatments, and restrictions in scope.

94

95 The complexity of climate change

96 The complex manner in which global climate change will affect local weather presents challenges for 97 climate change-ecosystem responses research. To mimic a future climate, factors such as air temperature, atmospheric CO₂, and precipitation need to be manipulated in combination, which can 98 99 be both conceptually and technologically challenging⁸. Therefore, a significant proportion of climate 100 change experiments have focused on measuring the effects of specific combinations of climate 101 factors (such as warming plus drought), manipulated using technology that was available or 102 affordable at that time (such as passive night-time warming and rain exclusion curtains)⁹. Although 103 these experiments have led to many invaluable outcomes, such approaches cannot fully cover the 104 complexity of climate projections or the covariance of meteorological variables. As such, they may,

105 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 106 moisture conditions and subsequent precipitation occurrence¹¹, increased frequencies of mild 107 droughts (including in spring and autumn), and increased frequency of heavy precipitation events¹². 108 109 These climate alterations can have a strong influence on ecosystem functioning: for example, decreased frost frequency may have a significant impact on plant mortality¹³ and more frequent mild 110 droughts can trigger plant acclimation and hence resistance to drought stress¹⁴. Therefore, many 111 112 climate change experiments did not simulate (i) an extreme event instead of a change in the mean 113 for a given single factor, (ii) regimes of events instead of a single event for a given single factor, and 114 (iii) complex coupling between multiple factors. This lack of refinement in climate manipulations 115 likely compromised the reliability of the estimation of ecosystem responses. Some steps have already 116 been taken to address this, by applying treatments of precipitation regime or heatwaves as observed in the field^{15,16} and by using translocation experiments, where macrocosms are displaced across 117 118 geographic gradients in order to expose them to other climates that match possible future conditions at the location of origin (space for time approach)¹⁷. However, such an issue cannot be solved by 119 120 modelling alone, because it requires testing too many possible interactions between factors, as well 121 as changing regimes of single factors.

122

123 Number and range of climate treatment levels

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

Also stemming from high equipment costs is the narrow range of climate treatments. Most experiments have kept this range within conservative boundaries²¹, presumably because more drastic (though realistic) climate treatments may have a catastrophic impact on a studied ecosystem, potentially leading to the loss of expensively equipped replicates. The truncation of more extreme climate conditions has, in turn, led to a lack of evidence regarding their effects on ecosystem functioning.

138 Finally, low temporal resolution is also an issue. Because it requires an extensive and high frequency 139 monitoring of ecosystem functions, a substantial proportion of climate change experiments have 140 only measured the ecosystem dynamics or trajectories annually or seasonally. Such experiments may fail to detect short-term dynamics of ecosystem responses²² or trajectories leading to a transition to 141 an alternative stable state^{23,24}. However, trends related to ecosystem dynamics often appear on 142 143 decadal time scales, because of the time needed to alter biogeochemical cycles and the properties of soil organic matter. Therefore the duration of the monitoring should be prioritized over its frequency 144 145 if the setup does not allow a good coverage of both.

146

147 Integration among disciplines

148 The very nature of climate change and its impacts is discipline-spanning and therefore requires an integrated approach²⁵. Althought the number of interdisciplinary studies related to climate change is 149 increasing steadily²⁶, there are still many challenges related to interdisciplinary research. These 150 include establishing common terminology, concepts and metrics^{25,27,28}, a consistently lower funding 151 success for interdisciplinary research projects²⁹, and a general lack of interdisciplinary research 152 153 positions²⁵. The barriers depend largely on the purpose, forms and extent of knowledge integration, and their combination³⁰. Although climate change research developed from multidisciplinarity to 154 interdisciplinarity, and further to transdisciplinarity³¹, most collaborative work in environmental 155

research is small-scale rather than large-scale interdisciplinary work³⁰. Small-scale integration refers 156 157 to collaborations between similar partners (for example, different natural science disciplines), while large-scale integration crosses broader boundaries (such as between natural and social science)³⁰. 158 159 Currently, ecosystem services studies are mostly limited to either the natural science aspects or the socio-economic science aspects and rarely cover the entire ecosystem services cascade³². This lack of 160 161 large-scale knowledge integration results in errors along this cascade; both when moving from 162 biodiversity and ecosystem functions to ecosystem services, and when moving from ecosystem 163 services to societal values.

164

165 **3. Recommendations**

166 Here we present potential ways to address these challenges: improving computational and

167 technological capabilities, increasing the number and range of climate treatment levels, and

168 employing an interdisciplinary approach.

169

170 Using climate model outputs and technology to refine climate change treatments

171 A first option to prescribe a projected change in weather dynamics is to alter specific characteristics 172 (such as drought duration, heat wave intensity) in isolation using high-frequency data of ambient 173 weather conditions so that they match future projections. The advantage of this method is that 174 atmospheric conditions can be modified with high-quality field data instead of relying upon less 175 precise regional climate model outputs with lower spatial and temporal resolution. Moreover, if used 176 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 177 178 combine two or more factors to provide information about interactions between climate 179 parameters.

180 Incorporating the complexity of projected changes can also be achieved by using outputs of state-of181 the-art climate models. Due to model biases, the appropriate model must be selected very carefully.

182 Global climate models (GCMs) are useful tools for assessing climate variability and change on global 183 to continental scales, typically with a spatial resolution of 100-250 km. To estimate climate variability 184 at more local scales, GCMs are dynamically downscaled using regional climate models (RCMs), which 185 resolve the climate at higher resolutions (typically 10-50 km). The GCM/RCM combinations can then 186 be chosen based on (i) how well models perform against local climate and weather characteristics in 187 the studied ecosystem and (ii) how representative future projections are to the multi-model mean. In 188 this case, one can simulate an ecosystem response to a given climate setup with higher accuracy. 189 However, unlike with a full factorial experiment, it is not possible to attribute an ecosystem response 190 to a given climate factor. Nevertheless, the model-output approach does facilitate the application of 191 increasingly high warming levels by using a global mean temperature gradient (see Section 4). It also 192 addresses the issues of covarying variables, and it can be directly linked with a scenario from the 193 Intergovernmental Panel on Climate Change which would represent a major step towards bridging 194 the gap between climate and ecosystem science.

195

196 However, to implement these options it is necessary to control climate conditions and atmospheric 197 composition with high frequency and high accuracy. This can be achieved only with dedicated and 198 advanced equipment. Ecotron infrastructures, which consist of a set of replicated experimental units 199 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 200 historically limited to a handful across the world⁹, but are becoming increasingly widespread³⁴⁻³⁶. 201 202 They also offer the opportunity to monitor ecosystem responses at sub-hourly frequencies, making it 203 possible to simultaneously discriminate between short- and long-term ecosystem responses.

204

205 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 208 quantitatively describing the relationship between a response variable and a continuous climate 209 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 210 211 nonlinearity, thresholds, and tipping points, and to interpolate and extrapolate ecosystem responses¹⁸. While such gradient designs should ideally be replicated, unreplicated regression 212 213 designs can be a statistically powerful way of detecting response patterns to continuous and 214 interacting environmental drivers, provided that the number of levels in the gradient is large enough³⁷. 215

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.

221

222 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.

234 Regarding the second step, economists need to be involved early in the process. Although there are 235 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 236 237 services that are considered most important to society. A common selection approach is to consider 238 the potential impact of ecosystem changes in terms of human welfare endpoints, often by means of 239 monetary valuation. Ecologists and economists must interact across disciplinary boundaries if 240 ecological experiments are intended to predict these endpoints within an ecosystem services 241 context⁴⁰. Hence, economists need to be involved during the design of ecological experiments in 242 order to ensure that those ecosystem service changes that are most relevant for human welfare are 243 measured and predicted.

244 We suggest that, the desired large-scale integration can be achieved in several steps, organized in a 245 top-down approach. The first step is to identify the key ecosystem services to value based on welfare 246 endpoints⁴¹. For most terrestrial ecosystems, this would imply assessing services from the following 247 list: food and raw material production and quality, water supply and quality, C sequestration, 248 depollution, erosion prevention, soil fertility, pest and pathogen control, pollination, maintenance of 249 biodiversity and recreation. The second step consists of identifying the set of variables that best 250 describes the ecosystem functions, processes and structures associated with these services. Based on the literature⁴², we suggest the following measures (see also Figure 3): (i) vegetation variables (plant 251 252 community structure, above/belowground biomass, litter quality), (ii) atmospheric parameters (net 253 ecosystem exchange, greenhouse gas emissions), (iii) soil abiotic (pH, texture, electrical conductivity, 254 macro-, micronutrient and pollutant content) and biotic (fauna and microbial community structure, 255 respiration, and biomass) variables, and (iv) all parameters that describe movements of water in the 256 soil-plant-atmosphere continuum (precipitation, leaching, air relative humidity, evapotranspiration, 257 water potential). Air and soil temperatures should also be monitored, since they determine 258 biogeochemical reaction rates. Finally, ecosystem processes, structures and functions need to be 259 translated into services, and ultimately into societal value by expressing them in monetary and non-

260 monetary terms. Measuring all of these variables, integrating them in an ecosystem service 261 framework, and estimating the societal value of these services would require expertise from plant 262 ecologists and ecophysiologists, hydrologists, soil biogeochemists, animal ecologists, microbiologists, 263 pedologists, climatologists, as well as modelers and environmental economists⁴³.

264

265 4. The UHasselt ecotron experiment as an initial application

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

268

269 Ecotron infrastructure

270 The UHasselt Ecotron facility consists of tightly controlled climate change manipulations of 12 271 macrocosms (soil-canopy columns of 2 m in diameter and 1.5 m depth), extracted without significant 272 disruption of the soil structure from a dry heathland plot in the 'Hoge Kempen' National Park (50° 59' 273 02.1" N, 5° 37' 40.0" E) in November 2016. The plot was managed for restoration six years before the 274 sampling. The design of this infrastructure benefited from exchanges through the AnaEE (Analysis 275 and Experimentation on Ecosystems)/ESFRI (European Strategy Forum on Research Infrastructure) 276 project. Some of the infrastructure's features were inspired by the Macrocosms platform of the CNRS 277 Montpellier Ecotron¹⁶. Each UHasselt Ecotron unit consists of three compartments: the dome, the 278 lysimeter, and the chamber. The dome consists of a shell-shaped dome made of highly PAR 279 (photosynthetically active radiation) transparent material, where wind and precipitation are 280 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-281 282 wave radiation are measured. The lysimeter (equipment for measuring hydrological variations 283 undergone by a body of soil under controlled conditions) contains the soil-canopy column, where 284 soil-related parameters are controlled (including the vertical gradient of soil temperature and water 285 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.icosri.eu/home), which provides real-time data on local weather and soil conditions, with a frequency of at least 30 minutes.

292

293 Climate manipulations

294 A double-gradient approach is adopted: one approach (six units) measures the effect of an altered 295 single factor (here, precipitation regime), while maintaining the natural variation of other abiotic 296 factors, and the other approach (six units) manipulates climate by jointly simulating all covarying 297 parameters, representing increasingly intense climate change. The two approaches are described 298 below. Because they sit isolated in an enclosed facility, it is possible that small initial differences in 299 the soil-canopy core in a given unit will increase with time to the point where it becomes statistically 300 different from the others. Therefore, the units were first distributed within the two gradients using a 301 cluster analysis to minimize the noise in ecosystem responses measured during a test period (see Fig. 302 S2) due to small-scale soil heterogeneity. This clustering was used to distribute the units according to 303 the pattern shown in Fig. 1.

304

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 yearlyprecipitation amount.

314 To drive the second gradient of the UHasselt Ecotron experiment, we use the climate variables 315 produced by an RCM following Representative Concentration Pathway (RCP) 8.5, a high-emission 316 scenario⁴⁶. The gradient itself is determined based on global mean temperature anomalies. In the six 317 units, climates corresponding to a +0 ° to +4 °C warmer world (projected for periods ranging from 318 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 319 320 comparison of the 'present-day' climate as simulated by the RCM (the +1 °C unit), to the unit driven 321 by ICOS field observations. Moreover, the climate simulated in the +1.5° C unit is reasonably 322 consistent with the lower end of the long-term temperature goals set by the Paris Agreement⁴⁸.

323

324 Integrating scientific disciplines for an interdisciplinary ecosystem service approach

325 As outlined in Recommendations, climate change experiments require large-scale knowledge 326 integration to enable more useful estimates of climate change effects on ecosystem functioning and 327 on society. The UHasselt Ecotron facility makes it possible to extend the degree of interdisciplinarity 328 by investigating the entire cascade from climate changes to ecosystem functions, ecosystem services, 329 and, finally, societal values. As such, the ecotron facility contributes to the development towards 330 large-scale knowledge integration on climate change. Consequently, the UHasselt Ecotron 331 experiment brings together several disciplines in an interdisciplinary framework (Fig 2). With input 332 from other involved disciplines, climatologists design the protocols for climate manipulations and 333 plant ecologists monitor plant communities in each ecotron unit. Numerical models for water 334 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 335 336 improve the power of this model by accounting for the soil community structure and species 337 interactions (food web). The specific role of soil organisms in soil biogeochemistry is investigated by 338 microbial and soil fauna ecologists. This is inferred from variation in responses of different functional 339 groups such as nitrogen fixers, mycorrhizal fungi and different feeding guilds of soil fauna, combined 340 with additional separate experiments, both in the field and in vitro. The outputs of the 341 measurements above (see Figure 3) allow experts in ecosystem ecology to quantify ecosystem 342 services. Environmental economists express the change in ecosystem services provided using bestpractice monetization approaches⁵⁰. For example, water quality regulation is assessed as the 343 prevented cost of intensified water treatment or use of other water resources. Measurements of 344 345 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 346 347 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. 348

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.

355

356 **5. Place of the design within the experimental landscape**

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.

362 Strengths and limitations of the design

363 The strengths of the suggested design comprises (1) high-performance microclimate conditioning, 364 both above- and belowground, which makes it possible to approximate field conditions while 365 maintaining control, (2) high-frequency automated measurements of ecosystem functions and thus 366 of treatment impact thereon, and (3) a large-scale interdisciplinary approach. The first two strengths 367 are inherent to the ecotron research infrastructure, while the large-scale integration can 368 theoretically be implemented in any climate change experiment. However, we consider ecotron 369 infrastructures to be particularly suitable for such an interdisciplinary approach, because of the high-370 end climate control and the broad range of functions monitored at a high frequency.

371 With respect to (1), studies focusing on ecosystem functions, processes and structures that are highly 372 sensitive to soil temperature and soil water potential would benefit most from being conducted in 373 ecotrons (for example, soil CO_2 exchange and C sequestration, growth and activity of soil microbes 374 and soil fauna), as the lysimeter component can generate very precise lower boundary conditions 375 and thus realistic vertical soil profiles of temperature and soil water status. With respect to (2), 376 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 377 378 parameters manually across long time scales. For example, simultaneous automated measurement 379 of the carbon, water and mineral nutrient cycles makes it possible to disentangle their interactions in 380 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.

387 Second, it may be difficult to financially support this type of experiment on the time scale of 388 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 projected climate change; this would allow for some extrapolation of ecosystem response in time (trajectories), which is possibly enough to estimate ranges of this response in the longer term.

393 Third, macrocosms in ecotron facilities are isolated from their ecosystem of origin. Hence genetic 394 input from propagules or pollination probably differ significantly from the field, which can be an 395 issue, especially in long-term experiments. This could be mitigated in two ways. The first is by 396 minimizing sampling disturbance, by sampling for soil microbes and soil fauna not more than twice a year, using 10 cm diameter soil cores, this would account for only 1.5% of total soil surface annually. 397 398 The second way is by replacing soil sampling cores in the lysimeter by cores taken from the same 399 ecosystem. This would also avoid holes at the soil surface that may alter water flow through the soil 400 column. Furthermore, field traps to collect airborne propagules can be collected yearly and their 401 content spread on the enclosed surface of the soil-canopy columns. These solutions would at least 402 ensure fresh genetic input into the system, even though this input may be different in the field in 403 future conditions.

Finally, radiation in ecotron enclosures sometimes differ than in the field. Artificial LED-lightning allows to control radiation precisely but is yet not able to reach the same radiation level as in the field, while ambient lightning can disrupt its synchronization with temperature or precipitation. This may be an issue while simulating heatwaves and droughts, which have more sunshine hours than wet periods ⁵⁴.

409

410 *Complementarity with other climate change experiments*

The weaknesses of the proposed design (small spatial scale, potentially insufficient time-scale, lack of interaction with the surrounding environment) can be mitigated further through the use of complementary experiments, which might even be partially integrated into the overarching approach. For example, owing to small spatial scale, the results might have limited validity as a 415 predictor of ecosystem responses at other sites and in other habitats. Running experiments in 416 parallel across multiple climates and locations with the same methodology, also known as 417 "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 418 design makes it possible to study plant response to nutrient addition and herbivore exclusion⁵⁶; and 419 420 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 421 422 Section 4, and testing the same climate gradient in different ecosystems across several ecotron 423 facilities would combine the high generalization potential of CDEs with the precision of ecotrons.

424 A second area for potential complementarity and integration is translocation experiments. These 425 experiments are well suited for long-term observations due to their relatively low funding 426 requirements and relative ease of implementation, and the soil macrocosms used in these 427 experiments are still connected to their surrounding environment¹⁷. However, the functioning of the 428 ecosystem is monitored less comprehensively and frequently within these types of experiments and 429 the influence of different climate factors on ecosystem functioning cannot be disentangled. 430 Consequently, running an ecotron and a translocation experiment in parallel on the same ecosystem 431 with similar climate treatments would make it possible to estimate the effect size of the connection 432 with the surrounding environment on ecosystem response to climate change. This information can 433 then, in turn, be used to correct the outputs of future ecotron experiments by accounting for the 434 isolation factor.

435

436 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}.

447

448 6. Conclusion

The effects of climate change on ecosystem functioning have far-reaching consequences for society. 449 450 Here we present a type of experiment that is designed to estimate the amplitude and dynamics of 451 ecosystem responses to climate change, and the consequences for ecosystem services. We foresee 452 that the holistic approach outlined in this Perspective article could yield more reliable, quantitative 453 predictions of terrestrial ecosystem response to climate change, and could improve knowledge on 454 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 455 456 ecosystem responses to help them decide on ecosystem management practices in the mid- and long-457 term, and that they will explain to policymakers and the wider public the societal impact of 458 ecosystem changes induced by climate change at a more detailed, ecosystem-specific level.

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460 Additional information

461 Correspondence and requests for materials should be addressed to F. R.

462

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471

472 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
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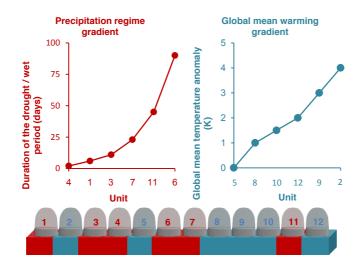
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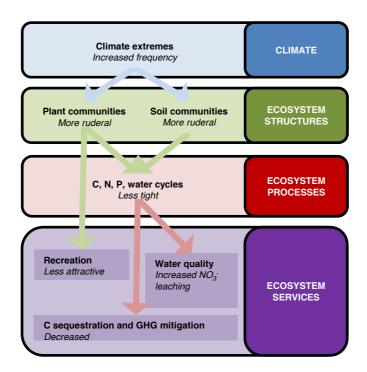
611

- 613 Figure captions
- 614 Figure 1. Overview of the two climate change gradient designs in the UHasselt Ecotron experiment.

615 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
- 617 1951-1955.
- 618
- 619 Figure 2. Impact pathway showing the reasoning behind the integration of scientific disciplines in the
- 620 UHasselt Ecotron experiment. The research hypotheses are given in italics and described in more
- 621 detail in Fig. S4.
- 622
- 623 Figure 3. Measured variables in the UHasselt Ecotron experiment and links with ecosystem functions,
- 624 services, and values. Left-hand side of the table: ecosystem services. Right-hand side: variables
- 625 measured in the ecotron experiment. Lower part of the table: illustration of how the societal value of
- 626 four of the ecosystems services will be assessed.
- 627





	Frequency of measurement	6 months	6 months	30 min	2 min	2 min	1 year	2 min	1 year	30 min	2 weeks	1 year	6 months	6 months	1 year	30 min	30 min	30 min	30 min	30 min		er resources			
MEASURED VARIABLES	Variable	Plant community structure	Shoot & root biomass	Net ecosystem exchange (NEE)	Temperature	GHG emissions (CH4, N2O)	Texture	Temperature	Biochemical composition	Electrical conductivity	Soil pore water chemistry	Available pollutant concentration	Fauna community structure	ers Microbial community structure	Mineralization rate	Precipitation	Leaching	Relative humidity	Evapotranspiration	Soil water potential	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	tional enjoyment
	Variable category	Variable category					Soil abiotic parameters						Soil biotic parameters					Water balance			ECONO	Prevented cost of in	Prevented damage	Non-use value of co	Use value of recreational enjoyment
	Pathogen control												0	0								\uparrow	\uparrow	\uparrow	\uparrow
	, Depollution											0					0								
	Soil fertility						0		0				0	0	0		0								
CES	Climate regulation Water retention						0	0		0	0					0	0	0	0	0					
ECOSYSTEM SERVICES	Recreation Climate regulation				0			0																	
EM ;	Maintenance of biodiversity		0																						_
SYS	Erosion prevention						0							0		0								-	
ECC	noitarteupes C		0	0		0			0																
	Vater quality	0	0							0	0					0	0	0	0	0					
	sleinətem weß	0	0																						
	Food	0	0																						