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Towards more predictive and interdisciplinary climate change ecosystem experiments

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1 **Improving the predictive power and interdisciplinarity of climate change experiments**

2

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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

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
82 and range of climate treatment levels, and employ an interdisciplinary approach to broaden the
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, we place this design 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 *The complexity of climate change*

92 The first challenge for research on climate change-ecosystem responses lies in the complex manner
93 in which global climate change will affect local weather. To mimic a future climate, factors such as air
94 temperature, atmospheric CO₂, and precipitation need to be manipulated in combination, which can
95 be both conceptually and technologically challenging⁸. Therefore, a significant proportion of climate
96 change experiments have focused on measuring the effects of specific combinations of climate
97 factors (such as warming plus drought), manipulated using technology that was available or
98 affordable at that time (such as passive night-time warming and rain exclusion curtains)⁹. Although
99 these experiments have led to many invaluable outcomes, such approaches cannot fully cover the
100 complexity of climate projections or the covariance of meteorological variables. As such, they may,
101 for example, under- or overestimate the effects on ecosystem functioning of changes in the
102 frequencies of frosts and heat waves, drought-heat-wave reinforcements¹⁰, interactions between soil
103 moisture conditions and subsequent precipitation occurrence¹¹, increased frequencies of mild
104 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

119 *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.

142

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 multidisciplinary 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

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

160

161 3. Recommendations

162 *Using climate model outputs and technology to refine climate change treatments*

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

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

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

187

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

196

197 *Increasing the number and range of climate treatment levels*

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

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

213

214 *Employing an interdisciplinary approach to better capture responses and interactions*

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

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

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

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

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

256

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

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

260

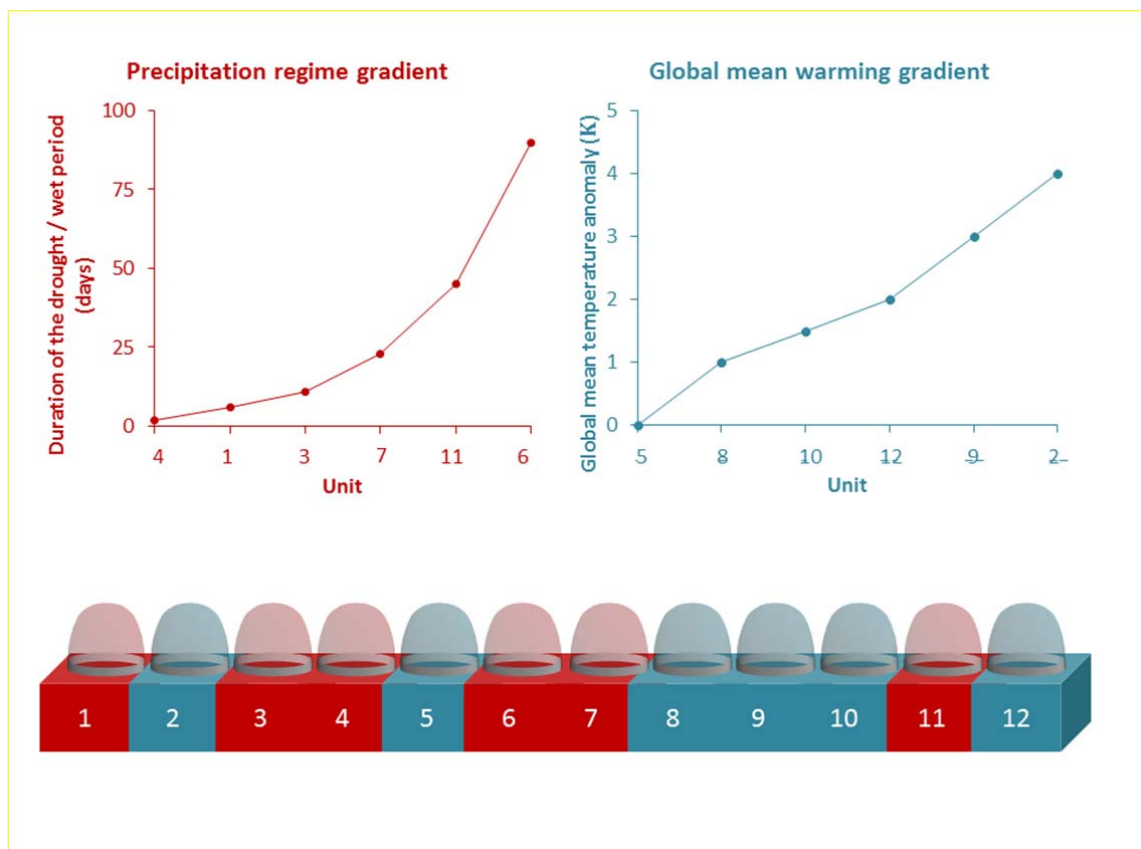
261 *Ecotron infrastructure*

262 The UHasselt Ecotron facility consists of tightly controlled climate change manipulations of 12
263 macrocosms (soil-canopy columns of 2 m in diameter and 1.5 m depth), extracted without significant
264 disruption of the soil structure from a dry heathland plot in the 'Hoge Kempen' National Park (50° 59'
265 02.1" N, 5° 37' 40.0" E) in November 2016. The plot was managed for restoration six years before the
266 sampling. The design of this infrastructure benefited from exchanges through the AnaEE (Analysis
267 and Experimentation on Ecosystems)/ESFRI (European Strategy Forum on Research Infrastructure)
268 project. Some of the infrastructure's features were inspired by the Macrocosms platform of the CNRS
269 Montpellier Ecotron¹⁶. Each UHasselt Ecotron unit consists of three compartments: the dome, the
270 lysimeter, and the chamber. The dome consists of a shell-shaped dome made of highly PAR
271 (photosynthetically active radiation) transparent material, where wind and precipitation are
272 generated and measured and where the concentration of greenhouse gases (CO₂, N₂O, CH₄), PPF
273 (photosynthetic photon flux density) and difference between incoming and outgoing short- and long-
274 wave radiation are measured. The lysimeter (equipment for measuring hydrological variations
275 undergone by a body of soil under controlled conditions) contains the soil-canopy column, where
276 soil-related parameters are controlled (including the vertical gradient of soil temperature and water
277 tension) and measured, and is weighed every minute. Suction cups and soil sensors are installed
278 following a triplicated 5 depth design (Fig. S1). The chamber is a gastight room that encloses the
279 lysimeter, where air pressure, air temperature, relative humidity, and CO₂ concentration are
280 controlled and key variables measured in each unit (Fig. S1). The UHasselt Ecotron is linked with a
281 nearby Integrated Carbon Observation System (ICOS) ecosystem tower ([https://www.icos-](https://www.icos-ri.eu/home)
282 [ri.eu/home](https://www.icos-ri.eu/home)), which provides real-time data on local weather and soil conditions, with a frequency of
283 at least 30 minutes.

284

285 *Climate manipulations*

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



296 *Figure 1. Overview of the two climate change gradient designs in the UHasselt Ecotron experiment.*
 297

298 *The units have been redistributed to maximize statistical similarity within a gradient prior to the*

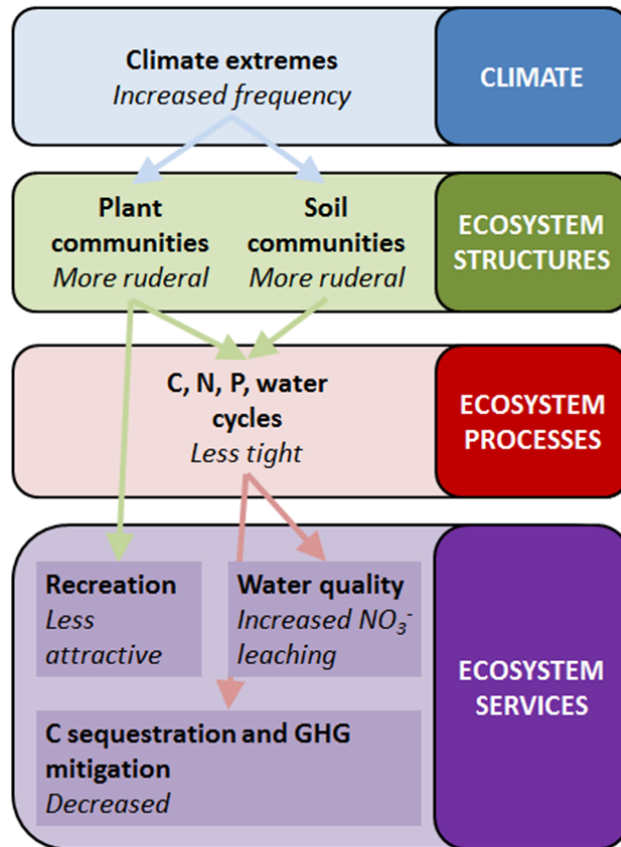
299 *treatment. Global mean temperature anomalies are computed with respect to the reference period*
300 *1951-1955.*

301

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

311 To drive the second gradient of the UHasselt Ecotron experiment, we use the climate variables
312 produced by an RCM following Representative Concentration Pathway (RCP) 8.5, a high-emission
313 scenario⁴⁶. The gradient itself is determined based on global mean temperature anomalies. In the six
314 units, climates corresponding to a +0 ° to +4 °C warmer world (projected for periods ranging from
315 1951–1955 to 2080–2089) are simulated (Fig. 1, Fig. S3), by extracting local climate conditions from
316 the RCM for periods consistent with these warming levels (Fig. S3)⁴⁷. This set-up also facilitates
317 comparison of the ‘present-day’ climate as simulated by the RCM (the +1 °C unit), to the unit driven
318 by ICOS field observations. Moreover, the climate simulated in the +1.5° C unit is reasonably
319 consistent with the lower end of the long-term temperature goals set by the Paris Agreement⁴⁸.

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

337

338 *Integrating scientific disciplines for an interdisciplinary ecosystem service approach*

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

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

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

369

370 Table 1. Measured variables in the UHasselt Ecotron experiment and links with ecosystem functions,
 371 services, and values. Left-hand side of the table: ecosystem services. Right-hand side: variables
 372 measured in the ecotron experiment. Lower part of the table: illustration of how the societal value of
 373 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	o							Shoot & root biomass	6 months
		o					o					Air parameters	Net ecosystem exchange (NEE)	30 min
													Temperature	2 min
													GHG emissions (CH4, N2O)	2 min
			o					o	o			Soil abiotic parameters	Texture	1 year
								o	o		Temperature		2 min	
		o								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	o	Soil biotic parameters	Fauna community structure	6 months
			o							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		

374

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

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

381 **Strengths and limitations of the design**

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

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

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

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

406 Second, it may be difficult to financially support this type of experiment on the time scale of
407 ecosystem responses (10 years or more)⁵³. Ecosystem shifts to alternative stable states may remain
408 undetected if the funding period is shorter than the period required for the ecosystem to shift. A
409 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.

428

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

436 “coordinated distributed experiments” (CDEs), would be better suited for this purpose as it allows
437 extrapolation and generalization of results while correcting for effect size⁵⁵. For example, such a
438 design makes it possible to study plant response to nutrient addition and herbivore exclusion⁵⁶; and
439 ecological responses to global change factors across 20 eco-climate domains using a set of
440 observatory sites⁵⁷. In fact, a coordinated distributed experiment using the design presented in
441 Section 4, and testing the same climate gradient in different ecosystems across several ecotron
442 facilities would combine the high generalization potential of CDEs with the precision of ecotrons.
443 A second area for potential complementarity and integration is translocation experiments. These
444 experiments are well suited for long-term observations due to their relatively low funding
445 requirements and relative ease of implementation, and the soil macrocosms used in these
446 experiments are still connected to their surrounding environment¹⁷. However, the functioning of the
447 ecosystem is monitored less comprehensively and frequently within these types of experiments and
448 the influence of different climate factors on ecosystem functioning cannot be disentangled.
449 Consequently, running an ecotron and a translocation experiment in parallel on the same ecosystem
450 with similar climate treatments would make it possible to estimate the effect size of the connection
451 with the surrounding environment on ecosystem response to climate change. This information can
452 then, in turn, be used to correct the outputs of future ecotron experiments by accounting for the
453 isolation factor.

454

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

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

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

466

467 **6. Conclusion**

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

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

486

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495

496 **Authors' contributions**

497 FR and RM took the lead in writing the manuscript and received input from all co-authors. The initial
498 conceptualization of this manuscript was discussed during a consortium meeting. All authors
499 proofread and provided their input to different draft versions and gave their final approval for
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501

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