

Do global change experiments overestimate impacts on terrestrial ecosystems?

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In recent decades, many climate manipulation experiments have investigated biosphere responses to global change. These experiments typically examined effects of elevated atmospheric CO₂, warming or drought (driver variables) on ecosystem processes such as the carbon and water cycle (response variables). Because experiments are inevitably constrained in the number of driver variables tested simultaneously, as well as in time and space, a key question is how results are scaled up to predict net ecosystem responses. In this review, we argue that there might be a general trend for the magnitude of the responses to decline with higher-order interactions, longer time periods and larger spatial scales. This means that on average, both positive and negative global change impacts on the biosphere might be dampened more than previously assumed.

A broad view on global change research

Global atmospheric change (including changes in temperature, precipitation, CO₂- and other trace gas concentration, and nitrogen deposition or soil conditions, henceforth ‘global change’) impacts on the biosphere involve a complex mixture of driver variables and will act on large spatial scales and long time scales [1,2]. Long-term assessments and predictions of these impacts on local, regional and global environments are typically carried out using models [3,4], which are both based on and tested against the results of experiments [5–9]. However, experiments are not only restricted in the degree of complexity that can be taken into account (here defined as the number of global change drivers manipulated simultaneously, normally one or two), but also in time (mostly < 10 years) and space (depending on vegetation height, typically a few square meters in grassland and a few hundred square meters in forests). Consequently, the validity of model predictions depends on how well results from these experiments represent larger scale responses. Here, we focus on the relative magnitude of responses in global change experiments

and relate it to the scale of the experiment (treatment complexity, time and space). We deliberately consider various driver variables (e.g. atmospheric CO₂ concentration, temperature and drought), response variables (e.g. NPP, litter fall and soil respiration) and ecosystems simultaneously in order to detect overarching patterns in biosphere responses to global change across different spatio-temporal scales. In the following, we develop our argument that there is evidence from experimental results for a general ‘dampening effect’ with increasing scale. We explore the three dimensions (1) treatment complexity, (2) time and (3) space and quantify their impact on the effect size of various response variables. We also discuss our hypothesis in the light of the results from ecosystem models. Our contribution originates in the belief that the numerous results reported from global change experiments and from ecosystem models over the past 30 years urgently call for syntheses, and the distillation of general response patterns, particularly because we are now well within the era of global change.

How do global change drivers combine?

The impact of global change drivers such as rising atmospheric CO₂, temperature and changes in precipitation on ecosystems are well studied when acting in isolation or with at most one interacting variable. For example, it is well known that elevated atmospheric CO₂ causes most plants to save water, e.g. [10]. We therefore expect that elevated CO₂ mitigates negative effects of drought, and can thus stimulate plant growth in water-limited environments [11,12]. In this example, we can argue that we understand how the two drivers interact mechanistically. If a third or fourth driver comes into play, understanding the mechanisms becomes much more difficult [13]. For example, how would the above system react if we also manipulated temperature, ozone concentration, species composition or herbivore pressure simultaneously? We could test this and look at a particular net response (with considerable effort), but would probably be unable to fully explain the mechanisms causing the response. Most

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experiments provide single factor responses, but how do they combine in the real world, where a multitude of drivers interact?

In order to investigate this question, we use an existing data base (160 climate manipulation sites; see www.ua.ac.be/wouter.dieleman, [14]), and pool a large range of driver variables (CO₂, irrigation and drought, temperature, ozone and soil conditions), response variables (aboveground, belowground and total biomass; litter fall; microbial biomass; microbial respiration; soil respiration; net N mineralization and soil C content) and various ecosystems. If the effect sizes of the response variables (% deviation from control treatment) are pooled and plotted against the number of tested driver variables, we observe that systems exposed to more than one global change driver simultaneously, on average show a smaller range of effect sizes (Figure 1a). The mean as well as the standard deviation of effect sizes tend to decrease with the number of involved drivers (Figure 1b). Nitrogen addition as a driver variable was excluded from the analysis to improve comparability to model results, which did not

include this major driver (see below). Also, the amount of added nitrogen in experiments often greatly exceeds natural nitrogen deposition. However, the inclusion of fertilisation as a driver does not change the picture much, except for producing a few outliers. A caveat is of course that very few experiments testing three global change drivers are available, and in those, there will be three single effects, three two-way interactions but only one three-way interaction, leading to a sharply decreasing sample size at the highest-level interactions (the same principle applies to two-factor experiments). To circumvent this, we used a non-parametric bootstrap (10 000 replicates from the original population, percentile confidence intervals) in order to obtain sample-size independent confidence intervals (95%) for the range of effect sizes. This shows that irrespective of the sample size, the range of effect sizes tends to decrease when multiple global-change drivers are tested simultaneously (insert in Figure 1a). We also tested whether the experimental conditions (greenhouse, open top chamber or field study) were responsible for this pattern, but this was not the case.

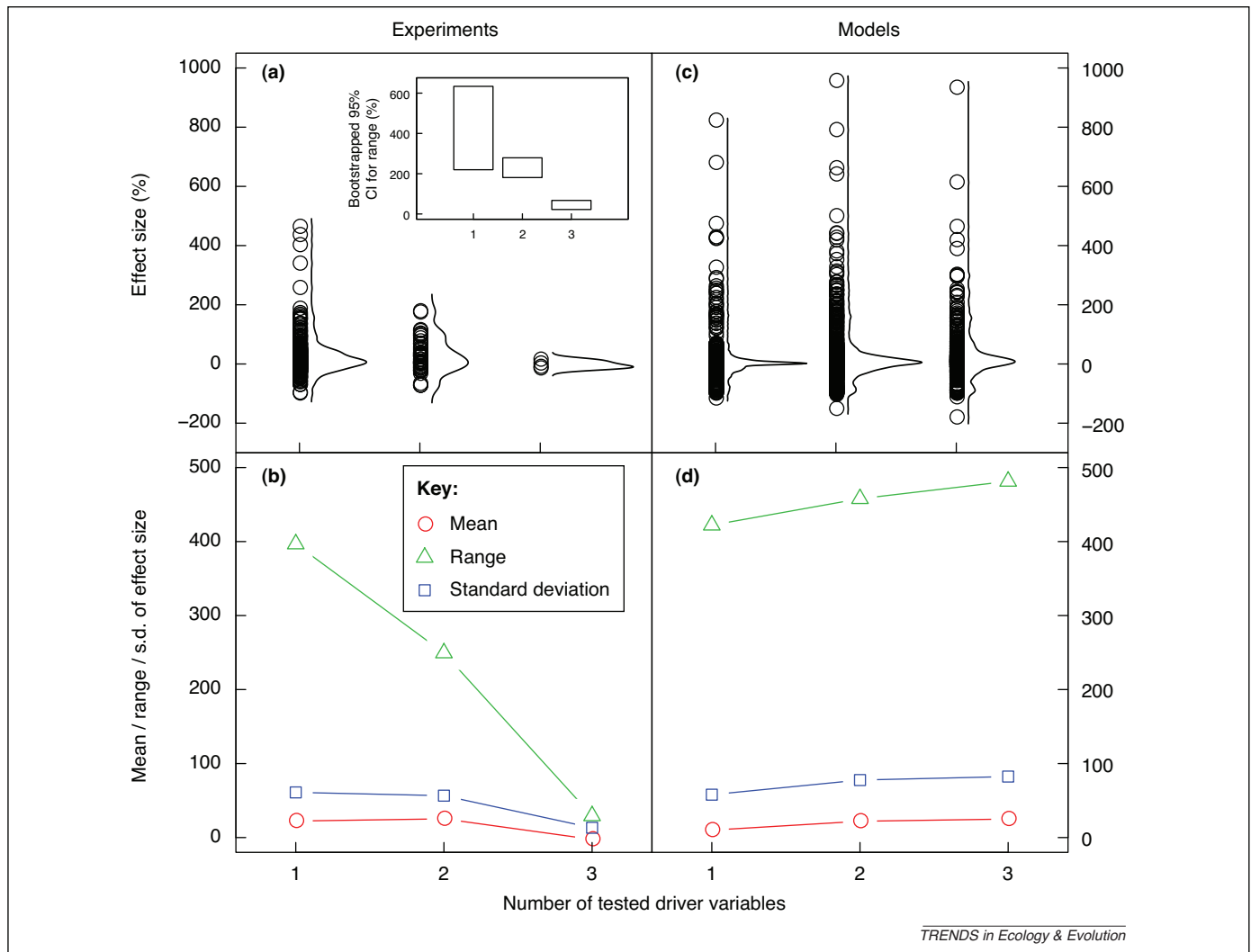


Figure 1. Effect sizes plotted against the number of tested driver variables irrespective of the nature of both the driver variables and the response variables. **(a)** The raw data from 160 experimental sites plus a relative density distribution using a spline function are shown ($n = 638$, 132 and 8 for one-, two- and three-factor experiments; www.ua.ac.be/wouter.dieleman, [14]). **(b)** The corresponding mean, range (spread of 99% of data) and standard deviation of effect sizes. Nitrogen addition was excluded as a treatment to improve comparability between experiments and models, but the inclusion of those studies would not change the overall picture. **(c and d)** The same plots for data from a modelling analysis with six ecosystem models, run for 17 driver variable combinations and seven sites: $n = 1176$, 1176 and 504, respectively, as in **(a)**. The insert in **(a)** shows the bootstrapped 95% confidence intervals for the ranges at each level.

In order to compare the above observation to results from ecosystem models, we use the comprehensive analysis of Luo *et al.* [4]. They ran four ecosystem models for seven different sites, testing 17 combinations of CO₂, precipitation and temperature treatments (see [4] for details). If these data are plotted as done for the experimental data above, a different pattern emerges (Figure 1c). Neither the mean, nor its standard deviation or the range of effect sizes decreased with the number of driver variables tested simultaneously. Certainly, this comparison does not rest on exactly the same driver and response variables, time spans and sites for the two cases, (and many more data points are available for model studies), but the discrepancy between experiments and models is strikingly obvious. A systematic stratification according to the nature of the driver and response variables did not identify individual drivers that might be responsible for the patterns seen in Figure 1.

Variation of effect sizes with the temporal and spatial scale

Much as we cannot reach perfectly realistic combinations of global change drivers in experiments, we are also restricted in the temporal and spatial scales we can cover. Very few global change experiments persist over long time periods (>10 years). We compiled all available studies that manipulate at least one global change driver over at least eight years (only four years of published stem growth data available for the Swiss Canopy Crane FACE site; SCC, response after eight years near zero, C. Körner *et al.* unpublished), again regardless of the response variables

measured. The combined data from three long-term studies with CO₂, soil warming and nitrogen addition [15–17] and three out of four forest FACE experiments (free air CO₂ enrichment) [18–21] suggest that the effect size of the response variable declines with time, either dying out or reaching a lower steady state value (Figure 2). In a natural system like the CO₂ springs in northern Italy (oak trees growing near geologically CO₂ degassing vents) for example, initial growth stimulation under elevated CO₂ gradually declined over 35 years [15]. Of course, models can be run for much longer time scales with relatively little effort. A direct comparison to experiments is not possible due to the much longer time spans considered, but there is evidence at least from some ecosystem models of a dampening effect e.g. in NEP (net ecosystem production) over the 21st century (average of six global ecosystem models [3]). This shows the capabilities of ecosystem models to account for processes leading to temporal effect dampening.

On the spatial scale, the spectrum ranges from laboratory experiments at the cellular or organism level to integrative experiments and approaches at a scale that captures the average response of many individuals over a large area. A well-studied example is the plant response to elevated CO₂ at the leaf (photosynthesis) and at the whole plant level (e.g. net growth response). It is generally observed that the leaf-level response (rate of photosynthesis) is consistently larger than the whole plant response [22–26]. Results from FACE experiments confirm this general trend [18,23,27–31]. Similarly, the water saving effect under elevated atmospheric CO₂ is reduced as we go from a first-order stomatal response to water savings at the

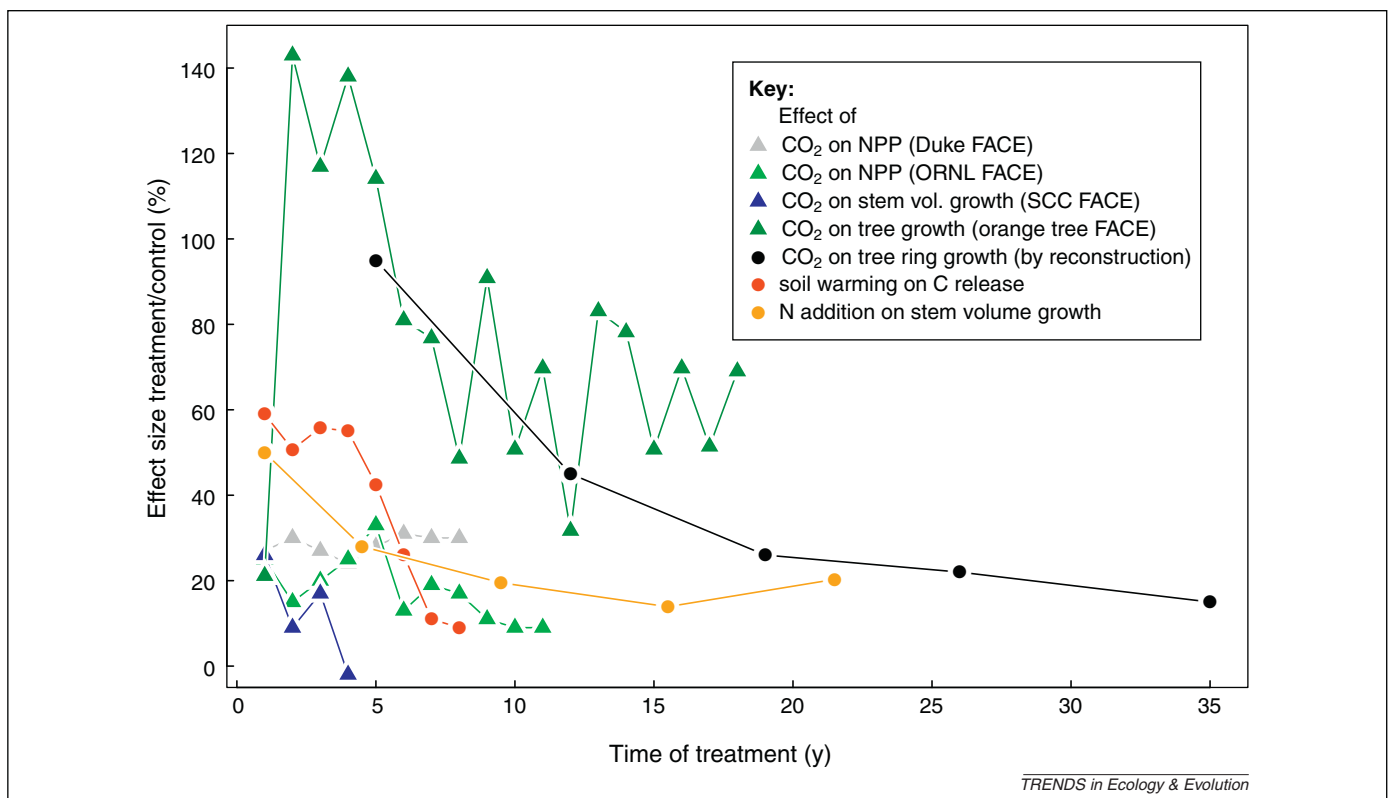


Figure 2. The impact of manipulation time on relative effect size measured in several long-term experiments [15–21]. Only mean trends are shown. Except for the Duke FACE study, there is an apparent decrease in the effect size over time.

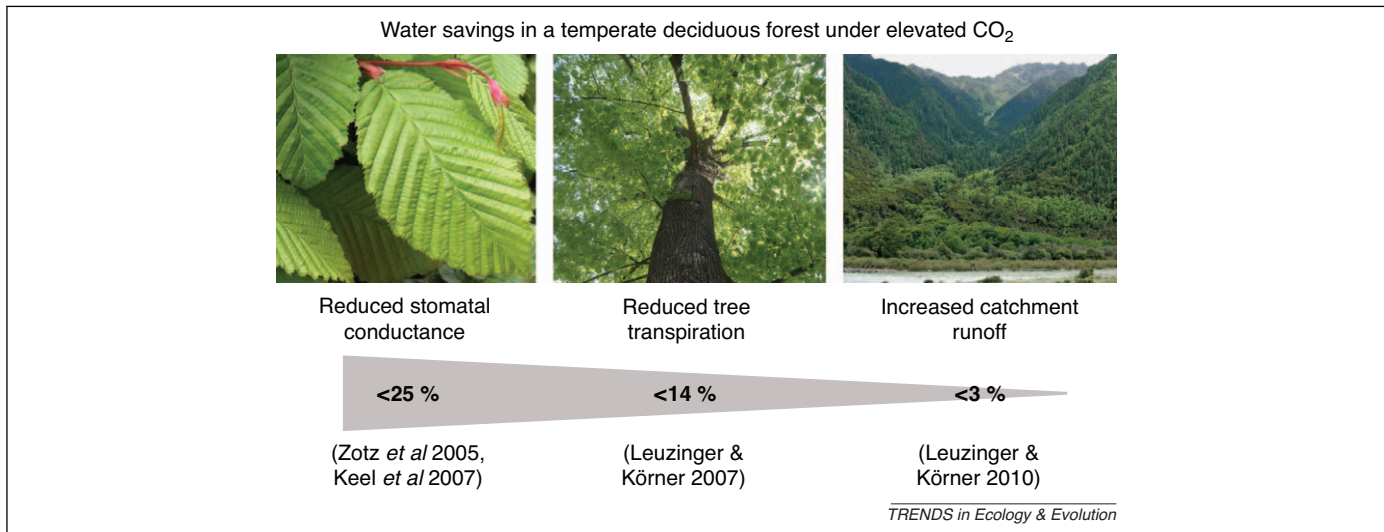


Figure 3. Case study at the Swiss Canopy Crane forest FACE site: 11 temperate broad-leaved trees were subjected to 550 ppm CO₂ during eight years near Basel, Switzerland. Shown are results from studies on water use of CO₂-treated and control trees (percentage change control to treated). At equal microclimatic conditions, the percentage reduced stomatal conductance corresponds approximately to the percentage reduced transpiration. The larger the spatial perspective of estimating water use under elevated CO₂, the smaller the response compared to the control scenario. One explanation for the observed phenomenon is the increasing number of relevant processes acting at larger scales (e.g. soil and atmosphere feedbacks, plant–animal interactions, and competition).

plant level and the net ecosystem response measured as increased runoff ([32–35], Figure 3). If we also consider the potential feedback from the atmosphere, we might find a further reduction of the CO₂ response [36]. This is a spatial scaling issue that is inherent to all FACE experiments: because the drier atmospheric conditions that would occur if all leaves in a landscape were subjected to elevated CO₂ should cause transpiration to increase again, the plot-scale response might be dampened even further. However, such an effect cannot be verified experimentally [36].

Why do effects fade with larger temporal and spatial scale?

A number of processes can be identified that might drive the system response to diminish over time. For example, a decreasing response of plant and microbial respiration to increasing temperature is a widely observed phenomenon. The mechanisms driving this so-called thermal acclimation are still an important topic of debate [37–41]. Likewise, decreased responses due to elevated atmospheric CO₂ result from decreasing nutrient availability associated with increased nutrient immobilization in plant biomass (progressive nitrogen limitation; e.g. [42]). The fact that most studies use step changes in the applied treatments might also contribute to an initially strong response [43]. This is because ecosystems might behave much like a pendulum that is displaced – the initial response is dampened subsequently. Genetic adaptation could also lead to effect dampening within relatively short time frames, even in trees [44]. Further, ontogenetic effects may contribute to effect size dampening within the duration of an experiment [45]. Finally, even if a positive response of a given species is sustained over time, shifts in species composition have the power to reverse initial trends. In grassland ecosystems, this has been observed within the experimental period [46]. A most remarkable signal dampening is to be expected from enhanced mortality rates following growth stimulation by CO₂: trees growing under elevated atmospheric

CO₂ might grow faster but live shorter, thus compensating first-order effects of increased carbon stocks [47,48]. Such biodiversity and population components in ecosystem responses are often overlooked.

Declining effect sizes with increasing spatial scale are understood in some cases. For example, it seems obvious that we cannot infer biomass increase from enhanced leaf-level photosynthesis due to elevated CO₂. However, the pathway of the additionally assimilated carbon from leaf to plant or ecosystem is still unclear [49,50]. Larger spatial scales could mean that a larger number of influential processes are in play and – if they cancel each other out rather than add up – this could explain the observed effect dampening. For example, if the carbon or water cycle is studied at the leaf level, we will miss many processes taking place in other plant parts such as symbiotic mycorrhizae or interactions with competing plants and animals. Therefore, if the aim of an experiment is the prediction of a net ecosystem response, the experiment should be conducted in as near-natural conditions as possible (e.g. using soil monoliths [51]).

Limitations of experiments and ecosystem models

In theory, we can think of different ways of how single-factor responses interact; if they are additive, both the range and the variance increase. If they are averaged (mean over all single-factor responses), the variance will decrease but both the mean and the range will remain constant. None of those simple models matches what is observed in Figure 1b and 1d. The obvious correlations between the single-factor responses and the two- and three-way interactions might be responsible for the sharp decrease in both range and variance of effect sizes but it is unclear why this should yield reduced effect sizes *per se*; one could just as well expect this correlation to cause larger effects. In contrast, models are apparently not able to account for the general trend of decreasing effect sizes at higher-level interactions. The observed overestimation

of effect sizes by models therefore most likely results from the way single-factor effects are combined. While we are aware that there will not be an easy solution to this, we think this might point to a crucial limitation of ecosystem models to accurately simulate interactions of multiple global change drivers. A possible solution to alleviate this would be to explicitly include a 'centre of gravity' in models that reflects the observed effect dampening, first attempts of such novel modelling approaches have been made recently [52]. In any case, we argue that adding mechanistic complexity to ecosystem models might complicate interpretability and traceability of model results, while improved model predictions are not warranted because we lack mechanistic understanding of the many interacting global change drivers.

The shown examples suggest that spatially confined, short-term or single factor experiments might tend to chronically overestimate net ecosystem responses. We do not challenge the importance and justification of such experiments. However, it is fundamental to understand what questions can be answered with an experiment. On the one hand, by studying responses of individual processes or parts of the ecosystem to short term, single treatments, we can aim to understand mechanisms, but not much can be concluded on the magnitude of long-term ecosystem responses. On the other hand, long-term, multifactor experiments can provide information to deduce a net ecosystem response with more confidence but at the same time limit inferences about the many underlying and interacting mechanisms.

Are the three phenomena related?

We argue that there is a strong link between the three scaling issues raised here: diminishing effect size with increasing levels of treatment complexity, longer duration and larger spatial scope of an experiment. If longer time periods and larger spatial scales are considered, this inevitably implies a growing number of processes acting on the system. On a temporal scale for example, rare weather conditions will only impact on a long-term experimental setup [53,54]. Such a rare weather event, however, might act similarly to a deliberately imposed drought treatment in a multifactor experiment; or, as mentioned above, larger spatial scales can mean the inclusion of processes beyond the scope of a small-scale experiment (e.g. feedbacks from soils and the atmosphere, inter- and intra-specific interactions, and plant–animal interactions). Again, such processes could act similarly compared to deliberately imposed treatments in a multifactor experiment. Therefore, it is not always clear which of the three described scaling phenomena causes the observed increase in the system's inertia in response to environmental perturbation.

We are aware that there are obvious counter examples to all three phenomena described here. For example, species shifts in forests will take longer than the duration of any experiment, and can cause a sharp change in a given response variable that cannot be captured short-term. Additionally, certain driver variables (e.g. elevated atmospheric CO₂ and nitrogen addition) probably yield higher responses in combination than they would indi-

vidually. However, we argue that overall, ecosystems might be more resilient to global change due to the described scaling issues, and that the latter are intrinsically related.

Conclusion

The observed effect size dampening with increasing scale and treatment complexity might reduce the long-term impact of the combined global change drivers relative to what is generally predicted. Results of global change experiments conducted at a given spatial and temporal scale are often (either implicitly or explicitly) extrapolated to higher levels of space, time or to a context containing other, hypothetical driver variables. However, small-scale experiments might fail to capture some of the processes and feedback mechanisms that occur on larger scales and therefore, as suggested here, might overestimate the true effect size. This means that both beneficial (e.g. a stimulation of plant growth under rising CO₂ or warming) and negative (e.g. reduced plant growth in response to drought) effects might be less dramatic than expected in the context of appropriate spatio-temporal scales and if several global change drivers are made to change concurrently. However, it is important to note that while effect dampening with scale and treatment complexity as suggested here might be part of intrinsic system behaviour, threshold effects, tipping points and biodiversity effects can also occur, e.g. [46,55]. It would therefore be wrong to downplay the risks associated with global change for terrestrial ecosystems based on our findings.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.tree.2011.02.011](https://doi.org/10.1016/j.tree.2011.02.011).

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