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Asymmetric warming significantly affects net primary production, but not ecosystem carbon balances of forest and grassland ecosystems in northern China

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We combine the process-based ecosystem model (Biome-BGC) with climate change-scenarios based on both RegCM3 model outputs and historic observed trends to quantify differential effects of symmetric and asymmetric warming on ecosystem net primary productivity (NPP), heterotrophic respiration (R_h) and net ecosystem productivity (NEP) of six ecosystem types representing different climatic zones of northern China. Analysis of covariance shows that NPP is significant greater at most ecosystems under the various environmental change scenarios once temperature asymmetries are taken into consideration. However, these differences do not lead to significant differences in NEP, which indicates that asymmetry in climate change does not result in significant alterations of the overall carbon balance in the dominating forest or grassland ecosystems. Overall, NPP, R_h and NEP are regulated by highly interrelated effects of increases in temperature and atmospheric CO_2 concentrations and precipitation changes, while the magnitude of these effects strongly varies across the six sites. Further studies underpinned by suitable experiments are nonetheless required to further improve the performance of ecosystem models and confirm the validity of these model predictions. This is crucial for a sound understanding of the mechanisms controlling the variability in asymmetric warming effects on ecosystem structure and functioning.

Historical observations over a large section of the earth's land area suggest that minimum temperatures (T_{min}) have increased significantly faster than maximum temperatures (T_{max}) since 1950 - a phenomenon commonly referred to as asymmetric warming[1–5]. These observations are further supported by climate change scenarios predicting faster increases in T_{min} than T_{max} particularly in mid to high northern latitudes and in arid regions[6,7]. At the same time, a growing body of evidence from long-term observations[8–13], manipulation experiments[14–18] and model simulations[19–21] has demonstrated differential impacts of increases in minimum and maximum daily temperatures on plant productivity and terrestrial ecosystems carbon budgets. However, most experiments have been conducted under diurnal constant (symmetric) warming simulations[22,23], and many models only use daily, monthly, or even annual mean temperatures for the temperature parameterizations when simulating and predicting the responses and feedbacks of terrestrial ecosystems to global warming[24,25]. In contrast, few studies have to date been conducted where the differential warming has been explicitly incorporated to examine the impact of the observed asymmetries on terrestrial ecosystem behaviors[20,26,27].

The effects of warming on plants and entire ecosystems also depend on interactions with other environmental factors such as precipitation, atmospheric CO_2 concentration, nitrogen depositions and general nutrient availability[28–30]. In addition, ecosystems located in different climatic zones are likely to respond differently to changes in these factors[12,13,31,32]. It is therefore important to understand the combined effects of asymmetric warming and changes in other environmental variables impact on fundamental metabolic ecosystem processes like photosynthesis and respiration.

Manipulative experiments are key tools to understand the mechanisms of ecosystem responses to climate change[22]. Nonetheless, establishing the impact of asymmetric warming on terrestrial carbon cycling in the field is a key challenge[32], and it is very difficult to simultaneously simulate the interactive effects of precipitation, elevated CO_2 and temperature[33]. Ecosystem modeling is therefore highly instrumental to stimulate hypotheses formulation and to extrapolate results from very limited, selected ecosystem settings across ecosystems, wider geographic areas and into the future[28].

In this study, we use a well-established process-based ecosystem model, Biome-BGC (BioGeochemical Cycles)[34], to compare the differential effects of symmetric and asymmetric warming on net primary productivity (NPP) and resulting carbon balances of six contrasting ecosystems in northern China. Our main objectives are to determine how plant productivity and ecosystem carbon sequestration are affected by temperature change asymmetries under various environmental change scenarios, and how these responses relate to variations in precipitation and atmospheric CO_2 concentrations.

Methods

Ecosystem processes are modelled using the Biome-BGC, which can simulate biogeochemical and hydrological processes of multiple biomes, using daily meteorological data including maximum, minimum and average temperature, precipitation, vapor pressure deficit, daylight average shortwave radiant flux density, and length of the day between sunrise and sunset[34]. Several further variables like the average daytime temperature (T_{day}) and average night-time temperature (T_{night}) are calculated from recorded maximum and minimum temperatures and meteorological principles[35], allowing for sunlight-dependent processes like photosynthesis to be driven by T_{day}, while processes such as decomposition are driven by 24 h averages. At the same time, maintenance respiration (R_m) of all living tissues is driven by changing temperature conditions throughout the day. R_m is calculated separately for sun and shade leaves and partitioned into night- and daytime respiration, with daytime respiration also needed to calculate net assimilation. R_m of sapwood is calculated separately for night and day respiration based on T_{night} and T_{day}, respectively. R_m of the root system finally is calculated based on the soil temperature, which is assumed to be the 11-day running weighted average of T_{day}. Overall, the simulated photosynthesis and respiration processes are sensitive to asymmetric temperature patterns and form the basis for the subsequent model outputs including Net primary productivity (NPP), heterotrophic respiration (R_h) and net ecosystem production ($NEP = NPP - R_h$). We selected a total of three forest and three grassland ecosystems varying in their temperature and precipitation regimes on the north sections of the North-South Transect of Eastern China and the east sections of the China Grassland Transect, respectively[36] (SI: Figure S1). The Biome-BGC model was adjusted for the six selected sites with a set of site-specific parameters (Table 1). Plant eco-physiological parameters were used according to White *et al.* (2000)[37], except where detailed site-specific data were available (SI: Table S1). Since the model does not currently simulate mixed forest stands, we divided the temperate mixed forests (TMF) site into evergreen needle-leaf forest (ENF) and deciduous broadleaf forest and simulated them separately[38]. The results were then added given different weights according to the basal area fraction covered by the respective plant functional types[39] (0.35 for the ENF and 0.65 for the deciduous broadleaf forest, respectively).

Our initial analytical focus was on the differences in ecosystem carbon budgets when comparing symmetric versus asymmetric climate change. For this, we used four different scenarios[20]: ambient scenario corresponding to the historical recorded temperature data during the period of 1961–1990 (T_{amb}), symmetric warming (T_{sym}), double asymmetric warming (T_{asy2}) and triple asymmetric warming (T_{asy3}). The three scenarios for temperature increases were based on a combination of recorded recent temperature increases (SI: Figure S2) and the predicted future magnitude of temperature increases simulated by a regional climate model (RegCM3) under the A2 IPCC CO_2 emission scenarios (SRES A2)[40] (SI: Figure S3). In the second step, the interactive effects of changes in temperature, precipitation, and atmospheric CO_2 concentrations were investigated. The precipitation treatment had two levels: an ambient level corresponding to the historical mean precipitation amounts recorded during the period of 1961–1990 (P_{amb}), and precipitation change based on the 2071–2100 predictions from the RegCM3 (P_{cha})[40]. The model MT-CLIM (Version 4.3) was used to compute meteorological variables not included in the standard weather station records and required by the Biome-BGC model[41]. The CO_2 treatment also had two levels: an ambient level corresponding to the historical concentrations recorded during the period of 1961–1990 (C_{amb}) based on the Mauna Loa measurements (http://co2now.org/), and a scenario taking into account the gradual predicted increase in atmospheric CO_2 concentrations from 626 ppm_v in 2071 to 836 ppm_v in 2100 (C_{inc}) as predicted by the SRES A2 emission scenario data[42].

Analysis of covariance was used to assess the effects of the different temperature treatments on NPP, R_h and NEP under the four scenarios, respectively. To avoid over-interpretation of modeled values, rigorous significance tests for the interactive effects of the three factors temperature, precipitation and atmospheric CO_2 concentration were not attempted. Instead, response patterns of each ecosystem were identified using the method outlined by Luo et al. (2008)[28].

Results

Net primary productivity (NPP). At most of our study sites, asymmetric warming is predicted to have a significant impact on NPP under the various environmental change scenarios (Figure 1).

Table 1 | Study site characteristics. Meteorological station location coordinates, elevation, and annual average temperature and annual precipitation statistics (means ± SD)

Vegetation type	Site	Location	Annual average temperature (°C)	Annual precipitation (mm)	Soil type (US soil classification-based)	Effective soil depth (m)	Soil texture (%)		
							Sand	Silt	Clay
Boreal coniferous forest (BCF)	Greater Khingan Mountains	50°50′ 121°30′ 826 m a.s.l.	−4.1 ± 0.9	442.8 ± 83.9	Brown coniferous forest soil	0.6	47	35	18
Temperate mixed forest (TMF)	Changbai Mountains	42°24′ 128°05′ 738 m a.s.l.	3.1 ± 0.8	722.4 ± 108.3	Dark brown forest soil	0.6	40	35	25
Warm-temperate deciduous broadleaf forest (DBF)	Dongling Mountains	40°24′ 115°30′ 1250 m a.s.l.	5.3 ± 0.7	575.2 ± 96.5	Mountain brown soil	1.0	20	50	30
Meadow steppe (MStp)	Changling county	44°42′N, 123°45′E, 145 m a.s.l.	6.0 ± 0.8	430.5 ± 107.3	Meadow chernozem	0.5	20	45	35
Typical steppe (TStp)	Duolun county	42°02′N, 116°17′E, 1324 m a.s.l.	2.8 ± 0.9	376.0 ± 70.5	Calcis-orthic Aridisol	0.6	53	27	20
Desert steppe (DStp)	Siziwang Banner	41°46′N, 111°53′E, 1456 m a.s.l.	3.6 ± 0.9	311.6 ± 72.7	Kastanozem	0.4	65	20	15

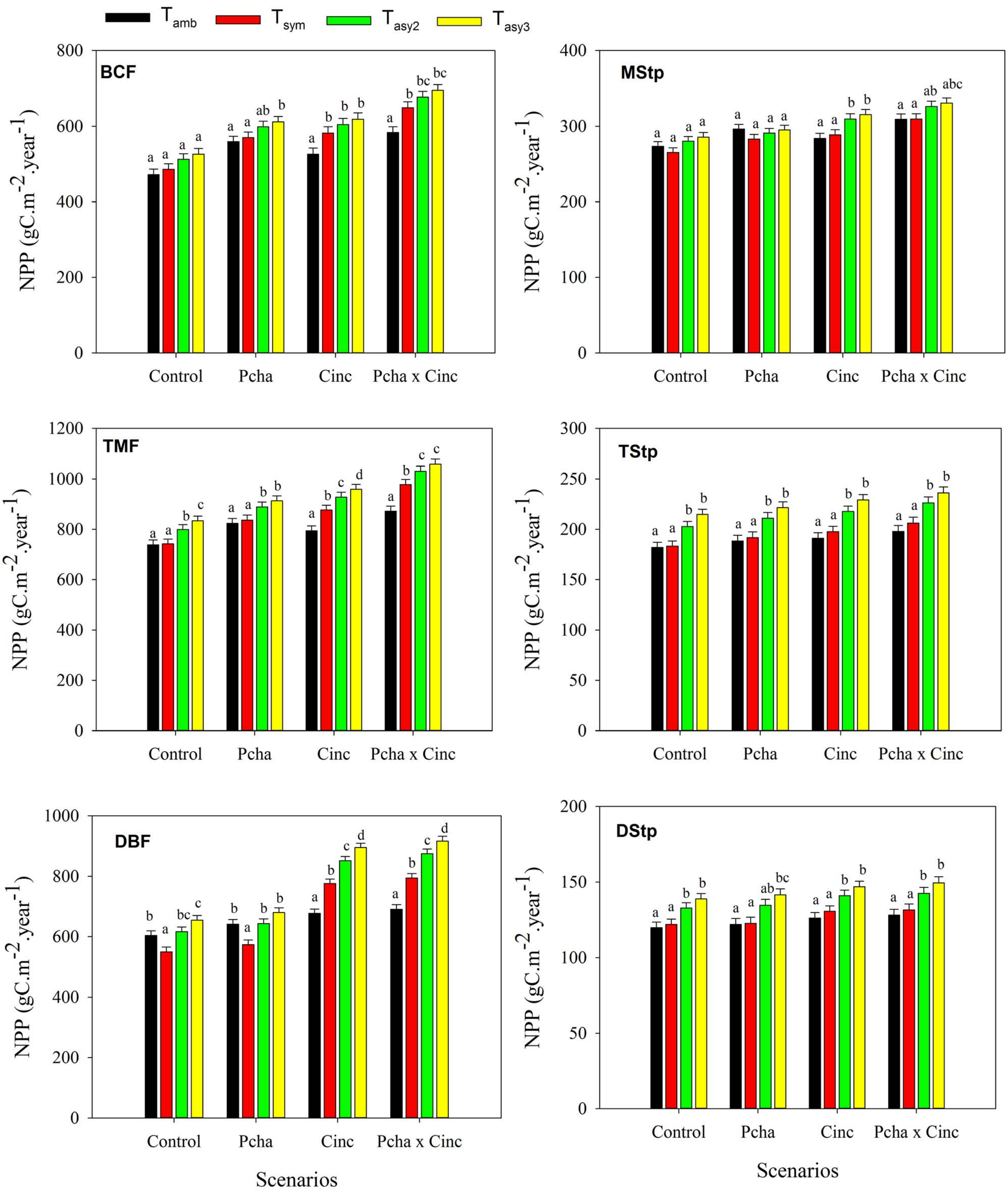

Figure 1 | Net primary productivity (NPP) response to the various temperature treatments under four environmental change scenarios, including the control, changes in precipitation amount (P_{cha}), gradual increases in concentrations of atmospheric CO_2 (C_{inc}) and their combinations ($P_{cha} \times C_{inc}$). Data are means ± standard error, differences letters bars indicate significant ($p < 0.05$) differences between means. (BCF: Boreal coniferous forest; TMF: Temperate mixed forest; DBF: Warm-temperate deciduous broadleaf forest; MStp: Meadow steppe; TStp: Typical steppe; DStp: Desert steppe)

Under the control scenario, a significantly lower NPP is predicted for T_{sym} than for both T_{asy2} and T_{asy3} scenarios for all ecosystems except for BCF and MStp. Furthermore, significant differences in NPP are computed between T_{asy2} and T_{asy3} scenarios for the two forest ecosystems TMF and DBF.

In scenarios taking into account predicted changes in precipitation (P_{cha}), NPP is significantly higher in both T_{asy2} and T_{asy3} in comparison to the T_{sym} scenario for TMF, DBF and TStp, while no significant differences are predicted between T_{asy2} and T_{asy3}. For BCF and DStp, NPP predictions are significantly higher for T_{asy3} in compar-

Table 2 | Relative strength of two- or three-way interactive effects on net primary production (NPP), heterotrophic respiration (R_h) and net ecosystem production (NEP)

Vegetation type	Scenarios*	NPP T_{sym}**	NPP T_{asy2}	NPP T_{asy3}	R_h T_{sym}	R_h T_{asy2}	R_h T_{asy3}	NEP T_{sym}	NEP T_{asy2}	NEP T_{asy3}
Boreal coniferous forest (BCF)	P_{cha}	−7.5	−2.1	−3.7	−22.4	−10.9	−7.2	53.0	41.2	18.1
	C_{inc}	144.8	99.4	77.9	71.4	48.1	41.4	115.7	122.0	96.1
	$P_{cha} \times C_{inc}$	27.2	29.5	35.1	49.3	40.7	37.1	−27.5	−18.3	6.6
Temperate mixed forest (TMF)	P_{cha}	11.7	6.1	−6.0	3.7	4.3	−0.7	14.5	−0.3	−13.7
	C_{inc}	264.1	134.1	91.5	−14.5	−10.5	−12.0	142.8	164.1	161.6
	$P_{cha} \times C_{inc}$	29.2	30.0	34.2	35.9	32.9	36.0	−21.3	−14.7	−12.8
Warm-temperate deciduous broadleaf forest (DBF)	P_{cha}	−30.2	−41.8	−27.5	−41.8	−24.4	−18.9	13.5	15.6	11.3
	C_{inc}	239.7	353.8	265.6	49.8	33.6	37.4	149.4	162.8	167.3
	$P_{cha} \times C_{inc}$	32.5	49.3	38.4	54.5	36.3	30.5	−14.2	−6.3	−5.6
Meadow steppe (MStp)	P_{cha}	−32.4	−82.2	−76.0	−18.7	−68.1	−65.6	−77.2	−44.0	−43.2
	C_{inc}	140.4	151.4	174.1	129.1	156.1	213.3	178.9	141.0	91.7
	$P_{cha} \times C_{inc}$	3.6	23.9	20.2	10.7	36.5	29.0	−34.9	−48.8	−27.3
Typical steppe (TStp)	P_{cha}	18.6	13.4	1.5	7.3	3.0	−2.8	−15.0	−13.2	−15.4
	C_{inc}	94.3	33.4	24.5	−51.1	−25.3	−19.7	30.8	31.5	47.1
	$P_{cha} \times C_{inc}$	−2.4	−0.3	−0.4	50.9	21.1	19.4	−1.5	−6.6	−30.3
Desert steppe (DStp)	P_{cha}	−31.0	−2.2	6.6	−31.1	−6.5	0.7	−11.8	4.6	15.8
	C_{inc}	55.6	24.4	13.8	−32.9	−18.0	−22.9	29.5	26.3	17.3
	$P_{cha} \times C_{inc}$	8.6	−3.4	0.3	28.7	13.5	0.9	−2.6	1.3	−1.8

*P_{cha}: changes in precipitation amount C_{inc}: gradual increases in concentrations of atmospheric CO_2 (C) and their combinations ($P_{cha} \times C_{inc}$).
**Tsym: symmetric warming; Tasy2: double asymmetric warming; Tasy3: triple asymmetric warming.

ison to the T_{sym} scenario. By contrast, the different warming treatments has no significant effect on NPP for the MStp.

When increases in CO_2 concentrations are taken into account (C_{inc} scenarios), NPP shows significant differences between all three warming scenarios for TMF and DBF in the rank order $T_{asy3} > T_{asy2} > T_{sym}$. NPP in T_{asy3} is also significantly higher than in T_{sym} for all three steppe ecosystems. In contrast, no significant changes in NPP for any of the three warming treatments are predicted for BCF.

Under the $P_{cha} \times C_{inc}$ scenarios, NPP shows significant differences between all three warming treatments for DBF in the order $T_{asy3} > T_{asy2} > T_{sym}$. NPP is also significantly higher under the T_{asy3} scenario in comparison to T_{sym} for TMF, TStp and DStp. No significant differences between scenarios are recorded for BCF and MStp.

Interactive effects of warming with C_{inc} on NPP are positive at all sites, while the magnitude of these effects varies (Table 2). However, the interactive effects of warming and P_{cha} are negative for DBF, MStp and DStp. The three-way interactions of warming with $P_{cha} \times C_{inc}$ are positive for BCF, TMF and DBF. The effects of the remaining two-way and three-way interactions are small in magnitude and not consistent among the three treatments at each site.

Heterotrophic respiration (R_h) and Net ecosystem productivity (NEP). Differences between simulated NPP and R_h are small when seen in relation to their overall magnitude, and the overall response pattern of modeled R_h in the different treatments (Figure 2) is similar to that for NPP. The three-factor combinations of T, C_{inc} and P_{cha} consistently stimulates R_h, whereas joining temperature regimes individually with either C_{inc} or P_{cha} does not cause consistent response patterns amongst the sites (Table 2).

The overall response patterns of NEP to the three warming treatments differs strongly to that modelled for NPP and R_h, with no significant differences resulting for the different temperature treatments under any of the various environmental change scenarios (control, P_{cha}, C_{inc}, or $P_{cha} \times C_{inc}$) (Figure 3).

Similar to the patterns of NPP, the interactive effects of temperature increases with C_{inc} are generally positive for NEP (Table 2). The interactive effects of warming and P_{cha} are positive for BCF, but negative for MStp. The three-way interactions of warming with $P_{cha} \times C_{inc}$ are chiefly negative for TMF and MStp. The other two-way and three-way interactions effects on NEP are small in magnitude and highly variable amongst warming treatments for each ecosystem.

Discussion

In agreement with reports based on historical data analyses[12] and local experimental observations from the TStp[16], our model suggests that NPP is significant larger when asymmetries are taken into consideration under various environmental change scenarios at the majority of our study sites. In the BIOME-BGC, day- and night-time warming could have different impacts on the NPP induced by the bias of climate forcing both directly via alterations of leaf processes and indirectly via changes in soil water availability and soil nutrient mineralization rates[34]. This pattern is underpinned by previous modeling simulations[19–21]. All these studies report that asymmetries in climate change patterns have a significant impact on ecosystem productivity, highlighting the great importance to include temperature change asymmetries in future experimental and model studies to realistically project responses and feedbacks of an ecosystem's carbon cycle to climate change[32–33]. With photosynthesis occurring during daylight hours and plant and microbial respiration occurring continuously, it could be expected that the latter is much more strongly affected by the strength of asymmetries[8,12,13]. Nonetheless, our model outputs indicate that NPP and R_h show fairly similar response patterns to temperature increases under the various environmental change scenarios at most of the study sites. As a consequence, NEP remains widely unaffected by the degree of asymmetric temperature change in the investigated ecosystems. This result indicates that increases in NPP cannot simply be equated to more carbon sequestration, as other ecosystem processes appear to counter-balance any NEP changes. More importantly, it also strongly suggests that processes of photosynthesis, respiration and carbon sequestration are considered as tightly linked, with photosynthesis and respiration appearing as entities closely coupled through carbon and nutrient supply and demand feedbacks[16]. Daytime warming alters net photosynthesis, which supplies the ecosystem with substrates for respiration at night. Night warming, however, does not only affect night-time ecosystem respiration, but may also stimulate plant compensatory photosynthesis during the following day by the depletion of leaf carbohydrates at night[14,16,43]. However, like most

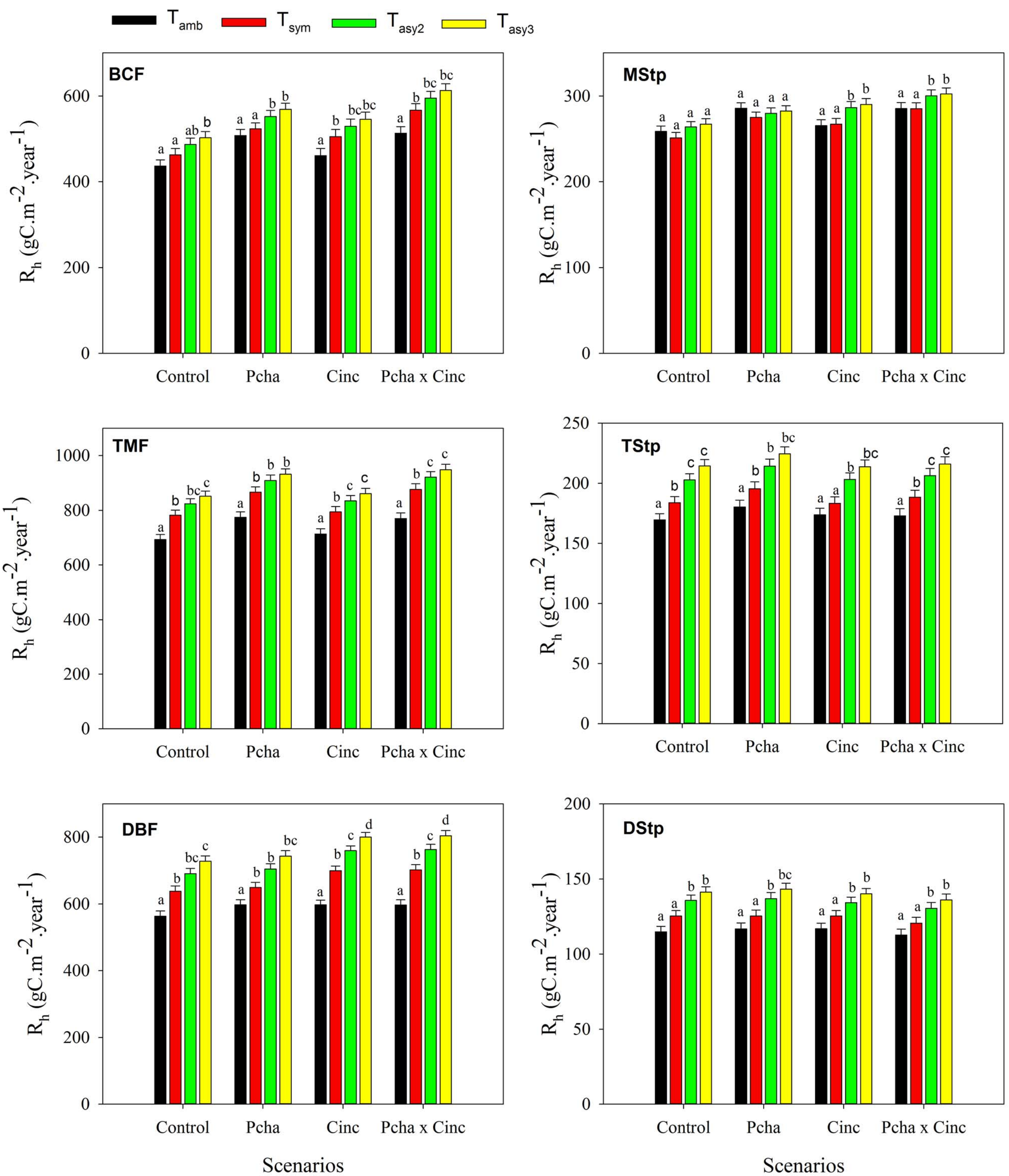

Figure 2 | Heterotrophic respiration (R_h) response to the various temperature treatments under four environmental change scenarios, including the control, changes in precipitation amount (P_{cha}), gradual increases in concentrations of atmospheric CO_2 (C_{inc}) and their combinations ($P_{cha} \times C_{inc}$). Data are means ± standard error, differences letters bars indicate significant ($p < 0.05$) differences between means. (BCF: Boreal coniferous forest; TMF: Temperate mixed forest; DBF: Warm-temperate deciduous broadleaf forest; MStp: Meadow steppe; TStp: Typical steppe; DStp: Desert steppe)

current biogeochemical models[13,32], BIOME-BGC cannot capture this 'photosynthesis over-compensation' phenomenon under asymmetric warming due to the missing implementation of the underlying ecophysiological response of plant photosynthesis to nighttime warming through altered draw-down of leaf carbohydrates at night. In addition to the different impacts on plant photosynthesis and ecosystem respiration, day- and night-time warming could have additional impacts on the plant community structure and composition[44–46], that further impact ecosystem productivity and carbon sequestration[47,48]. We therefore suggest that more attention should be paid to the structural and functional responses of carbon-related processes to changes in maximum and minimum day and night temperatures in the current generation of ecosystem models.

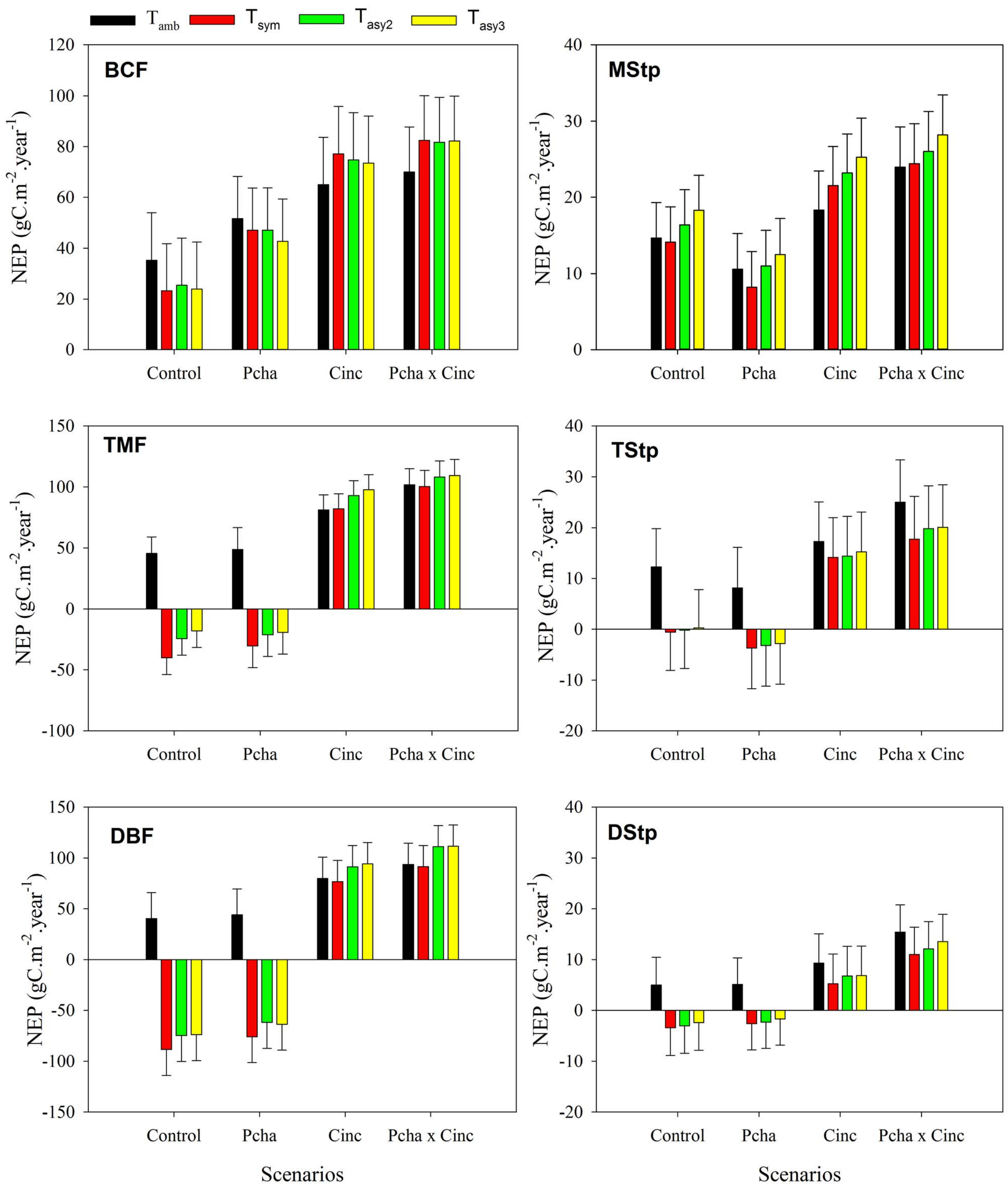

Figure 3 | Net ecosystem production (NEP) response to the various temperature treatments under four environmental change scenarios, including the control, changes in precipitation amount (P_{cha}), gradual increases in concentrations of atmospheric CO_2 (C_{inc}) and their combinations ($P_{cha} \times C_{inc}$). Data are means ± standard error. (BCF: Boreal coniferous forest; TMF: Temperate mixed forest; DBF: Warm-temperate deciduous broadleaf forest; MStp: Meadow steppe; TStp: Typical steppe; DStp: Desert steppe).

Our results indicate simple additive effects of the interactive effects of temperature, CO_2 concentrations and precipitation are rare, which is consistent with reports based on experiments manipulating temperature and atmospheric CO_2 concentrations[30]. Overall, single-factor response models may be misleading, creating unreliable predictions of ecosystem responses to multifactorial global change patterns, a trend already observed in temperature-focused experimental studies[16,27]. Our study further supports the need for more multifactorial experiments including not only the asymmetric shifts in temperature, but also the influence of precipitation regimes, nutrient availability and atmospheric CO_2 concentrations to improve predictions of ecosystems responses to global change[29,49] and allow an improved model parameterization and validity.

Models based on the interactions of all three factors considered in our study reveal substantial differences in the magnitude of effects between sites, which somewhat contradicts reports from earlier investigations[28]. This outcome highlights the importance of the local environment and ecosystem structure for the assessment of ecosystem carbon budgets and their response to asymmetric warming[11,13,32]. While the present analysis was restricted to a limited number of sites focused only on boreal and temperate ecosystems, we acknowledge that particularly the response of tropical and subtropical ecosystems to asymmetric warming is not well researched at present and merits further investigation.

1. Karl, T. R. *et al.* Asymmetric trends of daily maximum and minimum temperature. *B. Am. Meteorol. Soc.* **74**, 1007–1023 (1993).
2. Easterling, D. R. *et al.* Maximum and minimum temperature trends for the globe. *Science* **277**, 364–367 (1997).
3. Vose, R. S., Easterling, D. R. & Gleason, B. Maximum and minimum temperature trends for the globe: An update through 2004. *Geophys. Res. Lett.* **32**, L23822 (2005).
4. Zhou, L., Dickinson, R. E., Dai, A. & Dirmeyer, P. Detection and attribution of anthropogenic forcing to diurnal temperature range changes from 1950 to 1999: comparing multi-model simulations with observations. *Clim. Dynam.* **35**, 1289–1307 (2010).
5. Hartmann, D. L. *et al.* [Observations: atmosphere and surface] Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T. F. *et al.* (eds)] [159–254] (Cambridge University Press, Cambridge, 2013).
6. Lobell, D. B., Bonfils, C. & Duffy, P. B. Climate change uncertainty for daily minimum and maximum temperatures: A model inter-comparison. *Geophys. Res. Lett.* **34**, 5715 (2007).
7. Zhou, L., Dickinson, R. E., Dirmeyer, P., Dai, A. & Min, S. K. Spatiotemporal patterns of changes in maximum and minimum temperatures in multi-model simulations. *Geophys. Res. Lett.* **36**, L02702 (2009).
8. Alward, R. D., Detling, J. K. & Milchunas, D. G. Grassland vegetation changes and nocturnal global warming. *Science* **283**, 229–231 (1999).
9. Nemani, R. R. *et al.* Asymmetric warming over coastal California and its impact on the premium wine industry. *Clim. Res.* **19**, 25–34 (2001).
10. Peng, S. *et al.* Rice yields decline with higher night temperature from global warming. *P. Natl. Acad. Sci. USA* **101**, 9971–9975 (2004).
11. Zheng, H., Chen, L. & Han, X. The effects of global warming on soybean yields in a long-term fertilization experiment in Northeast China. *J. Agr. Sci.* **147**, 569–580 (2009).
12. Peng, S. *et al.* Asymmetric effects of daytime and night-time warming on Northern Hemisphere vegetation. *Nature* **501**, 88–92 (2013).
13. Tan, J. *et al.* Seasonal different response of photosynthetic activity to daytime and nighttime warming in the Northern Hemisphere. *Global Change Biol.* doi:10.1111/gcb.12724.
14. Turnbull, M. H. *et al.* Nocturnal warming increases photosynthesis at elevated CO_2 partial pressure in *Populus deltoides*. *New Phytol.* **161**, 819–826 (2004).
15. Volder, A., Gifford, R. M. & Evans, J. R. Effects of elevated atmospheric CO_2, cutting frequency, and differential day/night atmospheric warming on root growth and turnover of Phalaris swards. *Global Change Biol.* **13**, 1040–1052 (2007).
16. Wan, S., Xia, J., Liu, W. & Niu, S. Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. *Ecology* **90**, 2700–2710 (2009).
17. Bai, W., Xia, J., Wan, S., Zhang, W. & Li, L. Day and night warming have different effect on root lifespan. *Biogeosciences* **9**, 375–384 (2012).
18. Mäenpää, M. *et al.* Biochemical and growth acclimation of birch to night temperatures: genotypic similarities and differences. *Plant Biology* **15 (Suppl.)**, 36–43 (2012).
19. Rosenzweig, C. & Tubiello, F. N. Effects of changes in minimum and maximum temperature on wheat yields in the central US A simulation study. *Agr. Forest Meteorol.* **80**, 215–230 (1996).
20. Dhakhwa, G. B.& Campbell, C. L. Potential effects of differential day-night warming in global climate change on crop production. *Climatic Change* **40**, 647–667(1998).
21. Su, H. & Li, G. Simulating the response of the *Quercus mongolica* forest ecosystem carbon budget to asymmetric warming. *Chinese Sci. Bull.* **57**, 1544–1552 (2012).
22. Rustad, L. E. The response of terrestrial ecosystems to global climate change: Towards an integrated approach. *Sci. Total Environ.* **404**, 222–235 (2008).
23. Lu, M. *et al.* Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. *Ecology* **94**, 726–738 (2013).
24. Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187 (2000).
25. Shao, P., Zeng, X., Sakaguchi, K., Monson, R. K. & Zeng, X. Terrestrial carbon cycle: climate relations in eight CMIP5 earth system models. *J. Climate* **26**, 8744–8764 (2013).
26. Volder, A. *et al.* Does greater night-time, rather than constant, warming alter growth of managed pasture under under ambient and elevated atmospheric CO_2? *New Phytol.* **162**, 397–411 (2004).
27. Phillips, C. L., Gregg, J. W. & Wilson, J. K. Reduced diurnal temperature range does not change warming impacts on ecosystem carbon balance of Mediterranean grassland mesocosms. *Global Change Biol.* **17**, 3263–3273 (2011).
28. Luo, Y. *et al.* Modeled interactive effects of precipitation, temperature, and [CO_2] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biol.* **14**, 1986–1999 (2008).
29. Wu, Z., Dijkstra, P., Koch, G. W., Penuelas, J. & Hungate, B. A. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biol.* **17**, 927–942 (2011).
30. Dieleman, W. I. *et al.* Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature. *Global Change Biol.* **18**, 2681–2693 (2012).
31. Beier, C. *et al.* Carbon and nitrogen cycles in European ecosystems respond differently to global warming. *Sci. Total Environ.* **407**, 692–697 (2008).
32. Xia, J. *et al.* Terrestrial carbon cycle affected by non-uniform climate warming. *Nat. Geosci.* **7**, 173–180 (2014).
33. Still, C. As different as night and day. *Nature* **501**, 39–40 (2013).
34. Thornton, P. E. *et al.* Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agr. Forest Meteorol.* **113**, 185–222 (2002).
35. Running, S. W., Nemani, R. R. & Hungerford, R. D. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Can. J. Forest Res.* **17**, 472–483 (1987).
36. Yu, G. *et al.* Overview of ChinaFLUX and evaluation of its eddy covariance measurement. *Agr. Forest Meteorol.* **137**, 125–137 (2006).
37. White, M. A., Thornton, P. E., Running, S. W. & Nemani, R. R. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interact* **4**, 1–85 (2000).
38. Schmid, S., Zierl, B. & Bugmann, H. Analyzing the carbon dynamics of central European forests: comparison of Biome-BGC simulations with measurements. *Reg. Environ. Change* **6**, 167–180 (2006).
39. Wang, M., Guan, D., Hao, S. & Wu, J. Comparison of eddy covariance and chamber-based methods for measuring CO_2 flux in a temperate mixed forest. *Tree physiol.* **30**, 149–163 (2010).
40. Gao, X., Shi, Y. & Giorgi, F. A high resolution simulation of climate change over China. *Sci. China Earth Sci.* **54**, 462–472 (2011).
41. Thornton, P. E., Hasenauer, H. & White, M. A. Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria. *Agr. Forest Meteorol.* **104**, 255–271 (2000).
42. Nakicenovic, N. *et al.* Special report on emissions scenarios: a special report of Working Group III of the Intergovernmental Panel on Climate Change. Pacific Northwest National Laboratory, Richland, WA (US), Environmental Molecular Sciences Laboratory (US) (2000).
43. Xia, J., Han, Y., Zhang, Z., Zhang, Z. & Wan, S. Effects of diurnal warming on soil respiration are not equal to the summed effects of day and night warming in a temperate steppe. *Biogeoscience* **6**, 1361–1370 (2009).
44. Wu, Z., Dijkstra, P., Koch, G. W. & Hungate, B. A. Biogeochemical and ecological feedbacks in grassland responses to warming. *Nat. Clim. Change* **2**, 458–461(2012).
45. Xia, J. & Wan, S. The effects of warming-shifted plant phenology on ecosystem carbon exchange are regulated by precipitation in a semi-arid grassland. *PLoS ONE* **7**, e32088. doi:10.1371/journal.pone.0032088 (2012).
46. Penuelas, J. *et al.* Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global change biol.* **19**, 2303–2338 (2013).
47. Wang, S. *et al.* Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology* **93**, 2365–2376 (2012).
48. Liu, H. *et al.* Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. *Global change biol.* **19**, 2500–2510 (2013).
49. Chung, H. *et al.* Experimental warming studies on tree species and forest ecosystems: a literature review. *J. Plant Res.* **126**, 447–460 (2013).

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Author contributions

S.H. and S.W. planned and conducted the modelling, while S.H., S.W., F.J. and A.J. jointly wrote the manuscript.

Additional information

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