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 CO2 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.
tion and to extrapolate results from very limited, selected ecosystem settings across ecosystems, wider geographic areas and into the future25.

In this study, we use a well-established process-based ecosystem model, Biome-BGC (BioGeochemical Cycles)24, to compare the different 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 CO₂ 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 sunset34. 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 principles35, 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_{o} 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_{o}).

We selected a total of three forest and three grassland ecosystems varying in their temperature and precipitation regimes on the north sides of the North-South Transsect of Eastern China and the east sides of the China Grassland Transect, respectively26 (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 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 were used according to White et al. (2000)35, 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 separately36. The results were then added given different weights according to the basal area fraction covered by the respective plant functional types28 (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 scenarios26: ambient scenario corresponding to the historical mean precipitation amounts recorded at most of our study sites, wider geographic areas and into the future25. In this study, we use a well-established process-based ecosystem model, Biome-BGC (BioGeochemical Cycles)24, to compare the different 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 CO₂ concentrations.

**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).

| Site Location | Vegetation type | Soil type | Soil texture (%) | Annual average temperature (°C) | Annual precipitation (mm) | Effective soil depth (m) |
|---------------|----------------|-----------|------------------|---------------------------------|--------------------------|-------------------------|
| Dongling Mountains, 826 m a.s.l. | Broadleaf forest (BCF) | Fine loam | 0.5 47 35 18 | 4.2 8.8 83.9 | 3.1 ± 0.8 | 5.3 ± 0.7 |
| Changbaishan Mountains, 1530 m a.s.l. | Coniferous forest (CON) | Fine sandy loam | 0.6 40 25 30 | 5.0 11.5 169.3 | 6.6 13.0 255.7 |
| Jilin City, 145 m a.s.l. | Deciduous broadleaf forest (DBF) | Kastanozem | 0.4 65 20 15 | 3.1 6.6 72.7 | 6.0 12.0 243.0 |
| Changling county, 738 m a.s.l. | Tall steppe (TStp) | Medium loam | 0.5 40 35 20 | 4.3 9.4 167.3 | 6.0 12.0 243.0 |
| Duolun county, 1210 m a.s.l. | Typical steppe (TStp) | Medium loam | 0.5 40 35 20 | 4.3 9.4 167.3 | 6.0 12.0 243.0 |
| Siziwang Banner, 1456 m a.s.l. | Desert steppe (DStp) | Medium loam | 0.5 40 35 20 | 4.3 9.4 167.3 | 6.0 12.0 243.0 |

| Study site characteristics. Meteorological station location coordinates, elevation, and annual average temperature and annual precipitation statistics (means ± SD) |
|----------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Location                          | Site            | Vegetation type | Soil type       | Soil texture (%) | Annual average temperature (°C) | Annual precipitation (mm) | Effective soil depth (m) |
|----------------------------------|-----------------|-----------------|-----------------|-----------------|---------------------------------|--------------------------|-------------------------|
| Dongling Mountains                | Broadleaf forest (BCF) | Fine loam | 0.5 47 35 18 | 4.2 8.8 83.9 | 3.1 ± 0.8 | 5.3 ± 0.7 |
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| Duolun county                     | Typical steppe (TStp) | Medium loam | 0.5 40 35 20 | 4.3 9.4 167.3 | 6.0 12.0 243.0 |
| Siziwang Banner                   | Desert steppe (DStp) | Medium loam | 0.5 40 35 20 | 4.3 9.4 167.3 | 6.0 12.0 243.0 |
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-
Cinc are positive for BCF, TMF and DBF. The effects of the remain-

Warming scenarios for TMF and DBF in the rank order Tasy3 > Tasy2 > Tsym. The asymmetry in TMF and DBF in the order Tasy3 > Tasy2 > Tsym is also significantly higher than in Tsym 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 Pcha × Cinc scenarios, NPP shows significant differences between all three warming treatments for DBF in the order Tasy3 > Tasy2 > Tsym. NPP is also significantly higher under the Tasy3 scenario in comparison to Tsym for TMF, TStp and DStp. No significant differences between scenarios are recorded for BCF and MStp.

Interactive effects of warming with Cinc on NPP are positive at all sites, while the magnitude of these effects varies (Table 2). However, the interactive effects of warming and Pcha are negative for DBF, MStp and DStp. The three-way interactions of warming with Pcha × Cinc 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 (Rfh) and Net ecosystem productivity (NEP). Differences between simulated NPP and Rfh are small when seen in relation to their overall magnitude, and the overall response pattern of modeled Rfh in the different treatments (Figure 2) is similar to that for NPP. The three-factor combinations of T, Cinc and Pcha consistently stimulates Rfh whereas joining temperature regimes individually with either Cinc or Pcha 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 Rfh with no significant differences resulting for the different temperature treatments under any of the various environmental change scenarios (control, Pcha × Cinc or Pcha × Cinc) (Figure 3).

Similar to the patterns of NPP, the interactive effects of temperature increases with Cinc are generally positive for NEP (Table 2). The interactive effects of warming and Pcha are positive for BCF, but negative for MStp. The three-way interactions of warming with Pcha × Cinc 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 analyses12 and local experimental observations from the TStp16, 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 nighttime 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 rates34. This pattern is underpinned by previous modeling simulations19–21. 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 change32–33. 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 asymmetries8,12,13. Nonetheless, our model outputs indicate that NPP and Rfh 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 NPP 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 feedbacks52. 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 night54,16,43. However, like most

| Vegetation type | Scenarios | Tsym | Tasy2 | Tasy3 | Tsym | Tasy2 | Tasy3 | NEP |
|----------------|----------|------|-------|-------|------|-------|-------|-----|
| Boreal coniferous forest (BCF) | Pcha | -7.5 | -2.1 | -3.7 | -22.4 | -10.9 | -7.2 | 53.0 |
| | Cinc | 144.8 | 99.4 | 77.9 | 71.4 | 48.1 | 41.4 | 115.7 |
| | Pcha × Cinc | 27.2 | 29.5 | 35.1 | 49.3 | 40.7 | 37.1 | 27.5 |
| Temperate mixed forest (TMF) | Pcha | 11.7 | 6.1 | 6.0 | 3.7 | 4.3 | 0.7 | 14.5 |
| | Cinc | 264.1 | 134.1 | 91.5 | 14.5 | 10.5 | 12.0 | 142.8 |
| | Pcha × Cinc | 29.2 | 30.0 | 34.2 | 35.9 | 32.9 | 36.0 | 21.3 |
| Warm-temperate deciduous broadleaf forest (DBF) | Pcha | -30.2 | -41.8 | -27.5 | -41.8 | -24.4 | -18.9 | 13.5 |
| | Cinc | 239.7 | 353.8 | 265.6 | 49.8 | 36.3 | 37.4 | 149.4 |
| | Pcha × Cinc | 32.5 | 49.3 | 38.4 | 54.5 | 36.3 | 30.5 | 14.2 |
| Meadow steppe (MStp) | Pcha | -32.4 | -82.2 | -76.0 | -18.7 | -68.1 | -65.6 | -77.2 |
| | Cinc | 140.4 | 151.4 | 174.1 | 129.1 | 156.1 | 213.3 | 178.9 |
| | Pcha × Cinc | 3.6 | 23.9 | 20.2 | 10.7 | 36.5 | 29.0 | 34.9 |
| Typical steppe (TStp) | Pcha | 18.6 | 13.4 | 1.5 | 7.3 | 3.0 | 2.8 | -15.0 |
| | Cinc | 94.3 | 33.4 | 24.5 | -51.1 | -25.3 | -19.7 | 30.8 |
| | Pcha × Cinc | -2.4 | -0.3 | -0.4 | 50.9 | 21.1 | 19.4 | -1.5 |
| Desert steppe (DStp) | Pcha | -31.0 | -2.2 | 6.6 | -31.1 | -6.5 | 0.7 | -11.8 |
| | Cinc | 55.6 | 24.4 | 13.8 | -32.9 | -18.0 | -22.9 | 29.5 |
| | Pcha × Cinc | 8.6 | -3.4 | 0.3 | 28.7 | 13.5 | 0.9 | -2.6 |

*Pcha: changes in precipitation amount; Cinc: gradual increases in concentrations of atmospheric CO2 (C) and their combinations (Pcha × Cinc).

**Tsym: symmetric warming; Tasy2: double asymmetric warming; Tasy3: triple asymmetric warming.
current biogeochemical models\textsuperscript{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\textsuperscript{44-46}, that further impact ecosystem productivity and carbon sequestration\textsuperscript{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 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)
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.

Figure 3 | Net ecosystem production (NEP) response to the various temperature treatments under four environmental change scenarios, including the control, changes in precipitation amount ($P_{\text{rea}}$), gradual increases in concentrations of atmospheric CO$_2$ ($C_{\text{ma}}$) and their combinations ($P_{\text{rea}} \times C_{\text{ma}}$). 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 study reveal substantial differences in the magnitude of effects between sites, which somewhat contradicts reports from earlier investigations. 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 and allows improved model parameterization and further investigation.

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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.
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