
This is the **accepted version** of the article:

Wang, Songhan; Ju, Weimin; Peñuelas, Josep; [et al.]. «Urban–rural gradients reveal joint control of elevated CO₂ and temperature on extended photosynthetic seasons». *Nature ecology and evolution*, Vol. 3 (March 2019), p. 1076–1085. DOI 10.1038/s41559-019-0931-1

This version is available at <https://ddd.uab.cat/record/218190>

under the terms of the  **CC BY** COPYRIGHT license

1 **Urban–rural gradients reveal joint control of elevated CO₂ and temperature on**
2 **extended photosynthetic seasons**

3 Songhan Wang^{1,2,3}, Weimin Ju^{1,2}, Josep Peñuelas^{4,5}, Alessandro Cescatti⁶, Yuyu Zhou⁷,
4 Yongshuo Fu⁸, Alfredo Huete⁹, Min Liu^{10,11}, Yongguang Zhang^{1,2,3*}

5 ¹*International Institute for Earth System Sciences, Nanjing University, Nanjing, China.*

6 ²*Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and*
7 *Application, Nanjing, China.*

8 ³*Collaborative Innovation Center of Novel Software Technology and Industrialization, Nanjing, 210023,*
9 *China.*

10 ⁴*CSIC, Global ecology Unit CREAM-CSIC-UAB, Bellaterra 08193, Catalonia, Spain.*

11 ⁵*CREAF, Bellaterra 08193, Catalonia, Spain.*

12 ⁶*European Commission, Joint Research Centre, Directorate for Sustainable Resources, Ispra, Italy.*

13 ⁷*Department of Geological and Atmospheric Sciences, Iowa State University, Ames, IA 50011, USA.*

14 ⁸*College of water sciences, Beijing Normal University, Beijing, China.*

15 ⁹*School of Life Sciences, University of Technology Sydney, NSW 2007, Australia.*

16 ¹⁰*Institute of Eco-Chongming, Shanghai 200062, China.*

17 ¹¹*Shanghai Key Laboratory for Urban Ecological Processes and Eco-Restoration, School of Ecological*
18 *and Environmental Sciences, East China Normal University, Shanghai 200241, China.*

19 ***Corresponding author:**

20 Yongguang Zhang

21 International Institute for Earth System Sciences

22 Nanjing University

23 163 Xianlin Avenue, Qixia District, Nanjing, Jiangsu Province, China

24 Email: yongguang_zhang@nju.edu.cn

25 Tel. +86-(0)25-89681569

26 **Abstract**

27 Photosynthetic phenology has large effects on the land-atmosphere carbon exchange.
28 Due to limited experimental assessments, a comprehensive understanding of the
29 variations of photosynthetic phenology under future climate and its associated controlling
30 factors is still missing, despite its high sensitivities to climate. Here we develop an
31 approach that uses cities as natural laboratories, since plants in urban areas are often
32 exposed to higher temperature and carbon dioxide (CO₂) concentration, which reflect
33 expected future environmental conditions. Using more than 880 urban–rural gradients
34 across the Northern Hemisphere ($\geq 30^\circ$), combined with concurrent satellite retrievals of
35 sun-induced chlorophyll fluorescence (SIF) and atmospheric CO₂, we investigated the
36 combined impacts of elevated CO₂ and temperature on photosynthetic phenology at large
37 scale. Results show that in urban conditions of elevated CO₂ and temperature, vegetation
38 photosynthetic activity began earlier (-5.6 ± 0.7 days), peaked earlier (-4.9 ± 0.9 days)
39 and ended later (4.6 ± 0.8 days) than in neighboring rural areas, with a striking two- to
40 four-fold higher climate sensitivity than greenness phenology. The earlier start and peak
41 of season were sensitive to both the enhancements of CO₂ and temperature, whereas the
42 delayed end of season was mainly attributed to CO₂ enrichments. We used these
43 sensitivities to project phenology shifts under four “Representative Concentration
44 Pathway” (RCP) climate scenarios, predicting that vegetation will have prolonged
45 photosynthetic seasons in the coming two decades. This observation-driven study
46 indicates that realistic urban environments, together with SIF observations, provide a

47 promising way for vegetation physiological studies under future climate change.

48

49 Terrestrial ecosystems absorb approximately one quarter of the anthropogenic carbon
50 dioxide (CO₂) released into the atmosphere, which effectively mitigates climate warming¹.
51 The timing and duration of vegetation photosynthetic activity (i.e., photosynthetic
52 phenology), play an important role in the carbon cycle of land ecosystems^{2,3} and are
53 strongly affected by climate change⁴⁻⁷. Understanding the response of photosynthetic
54 phenology to increasing atmospheric CO₂ concentrations and global warming is,
55 therefore, essential to better understand the future dynamics of the terrestrial carbon
56 cycle^{8,9} and formulate land-based strategies to mitigate climate change¹⁰. Current
57 experimental assessments of the effects of climate warming and CO₂ fertilisation on plant
58 phenology have generally been restricted to manipulated experiments^{11,12} with very
59 limited spatial extent and species coverage, which may ultimately led to ambiguous and
60 controversial findings¹³. In particular, the role of CO₂ fertilisation on tree phenology
61 remains largely unknown in real natural settings. Moreover, many field experiments have
62 been recently terminated because of their high cost¹⁴, thus limiting consistent long-term
63 observations and reinforcing the need for effective, low-cost alternative monitoring
64 approaches.

65 In this analysis, we make use of contrasting conditions in urban–rural environments,
66 serving as “natural laboratories” to conduct a novel, and first time investigation on the
67 combined effects of future global warming and CO₂ fertilisation on vegetation phenology
68 at a very large scale¹⁴. Because of the urban heat island effect¹⁵ and the larger CO₂
69 emissions from fossil-fuel combustion¹⁶, vegetation in urban areas is typically exposed to

70 higher temperatures and CO₂ concentrations than in rural areas and are therefore
71 experiencing growing conditions projected for the future¹⁷. Assuming that phenology
72 responds similarly to altered temperature and atmospheric CO₂ in urban and rural areas,
73 the urban–rural gradients can be considered as “natural experiments” with similar
74 photoperiod and weather, and at lower costs¹⁴ than manipulation experiments. Using the
75 space-for-time substitution concept, we therefore used the physiological dynamics of
76 vegetation across urban–rural gradients to investigate the effects of future global warming
77 and CO₂ fertilisation on photosynthetic phenology. Data were collected from 880 urban
78 clusters and their adjacent rural areas at mid- to high-latitudes in the Northern
79 Hemisphere (NH, $\geq 30^\circ$) (Supplementary Fig. 1). Photosynthetic phenology was extracted
80 from the Orbiting Carbon Observatory-2¹⁸ (OCO-2) sun-induced chlorophyll
81 fluorescence (SIF, a proxy for photosynthesis) data, which are highly correlated with
82 photosynthetic rates and can monitor actual photosynthetic dynamics¹⁹. We used the
83 traditional, satellite greenness phenology for comparison, which was extracted from
84 Moderate Resolution Imaging Spectroradiometer (MODIS) Enhanced Vegetation Index
85 (EVI)²⁰. The urban–rural surface CO₂ gradients were obtained through a conversion
86 approach with OCO-2 column-averaged CO₂ mixing ratios (XCO₂) data (see Methods).
87 The primary objective of our analysis was to determine the differences in photosynthetic
88 phenology across urban–rural gradients and explore the combined effect of atmospheric
89 CO₂ enrichment and warming on plant photosynthetic phenology at a very large scale.
90 Phenological differences and environmental gradients were then used to quantify the

91 sensitivities of the processes and ultimately to project shifts in phenophases under
92 contrasting climate scenarios.

93 **Results**

94 We found that vegetation showed a larger than expected anticipation and
95 prolongation of the photosynthetic season within urban environments. On average, the
96 SIF-based photosynthetic activity began 5.6 days earlier, peaked 4.9 days earlier, ended
97 4.6 days later and lasted 10.2 days longer in urban than in rural areas (Fig. 1). These
98 variations were two- to four-times larger than those in greenness phenology derived from
99 MODIS EVI, due to the significantly higher urban–rural Δ SIF than Δ EVI during spring
100 and autumn (Supplementary Fig. 2). The timing of each phenological indicator we
101 examined (SOS, start of growing season; POS, peak of growing season; EOS, end of
102 growing season; GSL, length of growing season) was generally highly correlated between
103 urban areas and neighbouring rural counterparts, but with significant systematic
104 deviations, as indicated by the slopes of the regression lines (Supplementary Fig. 3). The
105 SOS and POS occurred earlier in urban areas as suggested by the slopes of larger than
106 one (i.e., 1.01–1.03 and 1.00–1.02; $p < 0.001$) for the regression lines, whereas the EOS
107 occurred later in urban areas as indicated by the slopes of lower than one (i.e., 0.98–0.99;
108 $p < 0.001$). On average within cities, SOS and POS were therefore advanced, while EOS
109 was delayed and GSL was extended for the phenology of SIF. Similar patterns were
110 found for the phenology of EVI, but the magnitudes of these changes were substantially
111 smaller than that of SIF (Supplementary Fig. 4) (about four-fold for Δ SOS and Δ POS,

112 two-fold for Δ EOS and three-fold for Δ GSL; Fig. 1). The larger differences of
113 photosynthetic phenology in urban–rural gradients than the differences of greenness
114 phenology were not affected by the mismatching in the spatial resolutions of SIF and EVI
115 data, as also tested after resampling to the same resolution (Supplementary Fig. 5). These
116 results suggest a remarkable shift in the response of photosynthetic phenology to urban
117 environmental conditions in the mid- to high-latitudes of the NH. These variations cannot
118 be completely explained by the variations in greenness phenology based on VIs or leaf
119 area index (LAI) and probably involve physiological responses to environmental drivers.

120 Vegetation in urban areas generally had earlier photosynthetic SOS and POS, later
121 EOS and longer GSL in the NH across various latitudes and climatic backgrounds (Fig.
122 2). On average, more than 70% of the urban clusters had longer photosynthetic seasons
123 than rural buffers. Δ SOS and Δ POS were lower than zero days across the whole NH,
124 while most of the Δ EOS were greater than zero days, suggesting that the trends of earlier
125 start/peak and delayed end of photosynthesis in urban environments are common across
126 northern latitudes. Nevertheless, some spatial patterns of phenological shifts along
127 urban–rural gradients were also evident; Δ SOS tended to decrease slightly as latitude
128 increased, Δ EOS and Δ GSL had the highest values at mid-latitudes, whereas Δ POS had
129 no clear trend (second column in Fig. 2). The spatial patterns of SIF Δ SOS were not fully
130 consistent with previous studies conducted with EVI, which showed an increasing trend
131 of EVI Δ SOS with the latitude²¹ due to the larger urban heat island effects in
132 high-latitudes^{15,22}. This divergence possibly suggests that the spatial distributions of SIF

133 urban–rural phenological gradients cannot be explained by temperature alone.
134 Importantly, urban–rural phenological differences were more significant in warm and dry
135 regions (i.e. areas with high mean annual air temperature and low annual precipitation)
136 than in other regions (third column in Fig. 2). Thus, the phenological differences in arid
137 climate zones were significantly higher than that in temperate and boreal areas
138 (Supplementary Fig. 6). These results suggest a general phenomenon that urban
139 environmental conditions extend the photosynthetic seasons and that the impacts in warm
140 and dry regions are greater than those in other climate regions.

141 Urban–rural phenological difference is likely driven by several interacting factors
142 including the enhancements of temperature and CO₂, the geolocation of a city, the urban
143 size and climatic background. Partial correlation analysis showed that SIF ΔSOS and
144 ΔPOS were mainly controlled by the daytime urban heat island (ΔLST_{day}) effects and
145 urban–rural CO₂ gradients (ΔCO₂), of which ΔLST_{day} was the most significant (Fig. 3).
146 SIF ΔEOS was mainly attributed to the enhanced CO₂ only, resulting in similarly
147 significant effects of temperature and CO₂ on ΔGSL (Fig. 3). In order to attribute the
148 effects of environmental drivers on photosynthetic phenology, we further analysed the
149 associations between elevated daytime temperature or atmospheric CO₂ and urban–rural
150 phenological differences (Fig. 4). The onset and peak time of photosynthesis were both
151 advanced significantly as atmospheric CO₂ concentration increased ($p = 0.013$ and 0.021 ,
152 respectively) and as temperature increased ($p = 0.019$ and 0.006 , respectively). The end
153 of photosynthetic activity was significantly delayed as CO₂ concentrations increased ($p =$

154 0.028), whereas its association with temperature was not significant ($p = 0.259$). Our
155 analyses suggest that not only daytime temperature but also atmospheric CO₂ have large
156 impacts on photosynthetic phenology of urban plants and, therefore, may potentially
157 inform on the future phenological shifts of natural vegetation under scenarios of warming
158 and atmospheric CO₂ enrichment.

159 Finally, using observations along the urban–rural gradients as natural laboratories,
160 we projected the shifts in photosynthetic phenology for the next two decades using the
161 space-for-time substitution. Based on forward stepwise regression models (see Methods),
162 the sensitivities of Δ SOS, Δ POS and Δ GSL to daytime temperature were -1.55 ± 0.60 ,
163 -2.11 ± 0.78 and 3.31 ± 1.10 days·°C⁻¹, respectively (Fig. 5a). The sensitivities of Δ SOS,
164 Δ POS, Δ EOS and Δ GSL to surface CO₂ concentration were -0.15 ± 0.07 , -0.18 ± 0.09 ,
165 0.17 ± 0.07 and 0.32 ± 0.11 days·ppm⁻¹, respectively (Fig. 5b). Given the observed
166 sensitivities and four different “Representative Concentration Pathway” (RCP) scenarios
167 of surface temperature and CO₂ concentration¹⁰ (i.e., RCP 2.6, 4.5, 6.0 and 8.5,
168 Supplementary Fig. 7), we projected the possible shifts of photosynthetic SOS, POS,
169 EOS and GSL from 2015 to 2035 (Fig. 5c-f). Results show that the phenophase shifts
170 were lowest in the RCP 2.6 scenario and highest in the RCP 8.5 scenario. Assuming
171 constant sensitivities for the next two decades, under the range of climate pathways
172 foreseen by RCP scenarios during 2015–2035, the photosynthetic SOS and POS would
173 advance at a rate of 2.8–5.7 and 3.3–6.9 days·decade⁻¹, respectively; and the EOS would
174 delay at a rate of 3.1–5.7 days·decade⁻¹, prolonging the growing season by a rate of

175 5.9–11.4 days·decade⁻¹ (Fig. 5g). It should be noted that the responses of vegetation
176 phenology to temperature are not stationary²³ and are likely to decline in the near
177 decades^{9,24}. Besides, the sensitivity of vegetation phenology to CO₂ may not be static
178 either in the coming decades, since the projected future concentrations of CO₂ could
179 exceed the range currently experienced by the urban vegetation (Fig. 4 & Supplementary
180 Fig. 7b). Therefore, our analysis of the projected photosynthetic phenology based on the
181 static sensitivity may overestimate the future shifts of vegetation phenophases. This
182 caveat, however, can be solved in the future by the same procedure introduced in this
183 study and continued satellite SIF observations.

184 **Discussion**

185 We found systematic differences between urban–rural gradients of photosynthetic
186 and greenness phenology (Fig. 1). The urbanization effects on vegetation photosynthetic
187 phenology were more than twofold higher than those on greenness. This phenomenon
188 could be explained by the significant differences between season cycle of EVI and SIF,
189 namely EVI shows an earlier spring increase and a later autumn falling than SIF
190 (Supplementary Fig. 2a). This difference has also been demonstrated by a recent study²⁵.
191 The timing of carbon assimilation in spring lags behind the leaf burst, which varies with
192 foliar structure and longevity²⁶. The photosynthetic activity shuts down before the
193 reduction of leaf chlorophyll and leaf abscission because of the limitation of light
194 availability²⁷⁻²⁹. Another possible reason is that urban phenology indicators from VIs are

195 suffering from mixed-pixel effects³⁰, which can bias the gradients of urban–rural
196 greenness phenology. Besides, VIs may have noisy signals from soil background, such as
197 soil color, artificial green building and other non-photosynthetic active materials,
198 especially in urban areas³¹⁻³³. On the other hand, originating from the vegetation
199 photosynthetic pigments, SIF is less sensitive to the soil background³⁴⁻³⁶.

200 Our analyses suggest that the urban–rural photosynthetic phenological differences
201 are mainly controlled by elevated atmospheric CO₂ concentration and daytime
202 temperature, while the differences of greenness phenology are mostly depending on the
203 urban size (Fig. 3). Previous studies using dozens of cities at regional scale suggest a
204 positive correlation between earlier greenup and surface temperature enhancement of
205 urban areas, such as in eastern North America^{37,38} and China^{21,39,40}. However, our analysis
206 show that the urban–rural greenness phenological differences are mainly correlated to the
207 urban size in the Northern Hemisphere, which is in line with a recent study conducted
208 with thousands of cities in the conterminous United States⁴¹. The positive relationship
209 between urban–rural greenness phenological gradients and urban size (an indicator of
210 urbanization), may result from the shifts of vegetation percentages and regional climate
211 conditions induced by urban expansion⁴¹. On the contrary, the earlier start and peak of
212 photosynthesis activity inferred from SIF observations have a significant correlation with
213 elevated temperature in urban areas (Fig. 4a&b). This discrepancy might partly relate to
214 the different sensitivity of VIs and SIF to temperature increases, either from satellite
215 data²⁵ or previous site-level study⁴². More importantly, SIF has a positive correlation with

216 GPP both in leaf-level and site-level^{19,43,44}, which is a more direct indicator of vegetation
217 physiological status than VIs⁴⁵. Seasonality of SIF from ground-based measurements⁴⁶,
218 tower-based observations⁴⁷ and satellite-based data²⁵ generally has high correlations with
219 that of GPP. Therefore SIF-based photosynthetic phenology in studies of “urban
220 laboratories” could provide a better proxy of the actual vegetation photosynthetic changes
221 in response to the climate change than VIs, which provide proxies of vegetation
222 greenness.

223 Using 880 cities, our results confirm that vegetation photosynthesis activities in
224 spring are triggered by daytime temperature, not by nighttime temperature⁸ (Fig. 3).
225 However, the sensitivity of SOS to daytime temperature in this study (1.55 ± 0.60 days
226 per °C) is lower than previous studies for boreal and temperate forests based on longtime
227 satellite VIs or ground observations^{8,9,48-52}. This may reflect the declining warming effects
228 on spring leaf unfolding⁹ and weakening temperature control on the interannual
229 variations of vegetation spring carbon uptake⁵³. The reduced sensitivity of spring leaf
230 unfolding to temperature may partly result from the reduced chilling accumulation in
231 urban areas⁹, in which the winter temperatures may become insufficiently low to meet the
232 requirement of chilling due to the urban heat island effects. Photoperiod may also
233 influence the warming effects on spring phenology, although its impact remains unclear
234 and is under debate^{5,23,54,55}. We also found that the photosynthetic POS have an earlier
235 trend (about 3.3–6.9 days per decade) in the near decades, which is consistent with the
236 POS trend of $\delta^{13}\text{C}$ data (about 4.3 ± 2.9 days per decade)⁵⁶, and are larger than the POS

237 trends from NDVI data or ground phenology measurements^{48,56,57}. This phenomenon
238 highlights the advantages of SIF for tracking vegetation seasonal photosynthetic activities
239 and carbon uptake. Our analysis also reveals a delayed end of vegetation photosynthesis
240 in urban areas (Fig. 1). Other than the earlier start of SOS and its response to global
241 warming, our understanding of the drivers for delayed EOS is still limited.
242 Temperature^{12,58}, photoperiod⁵⁹, elevated atmospheric CO₂⁶⁰ and spring phenology⁶¹ were
243 claimed to be associated to this delayed vegetation senescence. Nevertheless, our analysis
244 suggests a pronounced delay in the end of vegetation photosynthesis in urban
245 environments and these delays are highly correlated to the elevated atmospheric CO₂
246 concentration.

247 Current studies generally focus on the responses of phenophases to warming^{9,13},
248 ignoring the importance of additional environmental drivers. From this point of view our
249 analysis highlights that photosynthetic phenological shifts are not only controlled by
250 daytime temperature but also by atmospheric CO₂. CO₂ fertilisation seems to have a large
251 effect on the advancement of photosynthetic activity, particularly under warm and dry
252 conditions; and the delayed end of photosynthesis is mainly attributed to the elevated
253 atmospheric CO₂ rather than temperature, which is consistent with field experiments⁶²⁻⁶⁴.
254 The delayed EOS may be because photosynthesis could be sustained for longer period in
255 the absence of sink limitations under elevated atmospheric CO₂ concentrations⁶⁴. Direct
256 evaluations of the future projected phenophase shifts are difficult, however, given a
257 global increase in CO₂ concentration of 16.5 ppm·decade⁻¹ and temperature of

258 0.16 °C·decade⁻¹ in the past three decades⁶⁵ (1982–2011), our estimates of the prolonged
259 photosynthetic growing seasons (5.5 ± 2.1 days·decade⁻¹) are significantly higher than
260 current estimates (2.2 to 3.9 days·decade⁻¹) based on long-term satellite vegetation
261 indices^{66,67} and the *in situ* experimental results based on greenness observations from a
262 recent study⁵. Our results suggest that the sensitivity of photosynthetic phenology to
263 climate is strikingly higher than that of traditional greenness phenology, and therefore,
264 that the current methods based on satellite VIs and *in situ* greenness observations are
265 likely to underestimate the extension of carbon sink period under climate change.
266 Crucially, our results show that, with increasing atmospheric CO₂, the growing seasons
267 are likely to expand in the next two decades, which in turn might contribute to an
268 increasing trend of the terrestrial carbon sink and generate an important negative
269 feedback in the climate system.

270 Yet it should be noted that some limitations still remain in our analysis. Landscape
271 configuration, species composition⁶⁸, atmospheric deposition (e.g., nitrogen and
272 phosphorus), air pollutants (e.g., ozone), management practices and hydrological regimes
273 may also affect urban–rural phenological differences. These factors may have complex
274 and to some extent counterbalanced impacts on vegetation photosynthesis in urban
275 environments. For example, urban areas generally receive higher rates of atmospheric
276 nitrogen and phosphorus deposition⁶⁹, which may positively contribute to urban–rural
277 phenological differences (Supplementary Fig. 8b). On the other hand, urban areas
278 typically show higher daytime ozone concentrations that can be detrimental to

279 photosynthesis⁷⁰, and these urban–rural ozone differences may negatively contribute to
280 the urban–rural phenological differences (Supplementary Fig. 8c). Besides, vegetation
281 species and human management practices may vary between urban and rural areas; and
282 apart from the temperature and CO₂, water stress indices such as precipitation, vapour
283 pressure deficit (VPD) and soil moisture, may also have influences on the vegetation
284 phenology⁷¹⁻⁷³. Urban–rural phenological gradients in areas with low precipitation are
285 generally more pronounced (Supplementary Fig. 8a), because vegetation in urban areas is
286 likely to be affected by irrigation and thus not limited by water supply. To test whether
287 our results were affected by the irrigation of urban vegetation, we repeated the analysis
288 after excluding the cities in the arid climate zones, assuming that the irrigation effect on
289 urban–rural phenology gradients could be more significant in these areas. Results also
290 showed that the extended photosynthetic seasons in urban areas were both controlled by
291 the elevated temperature and CO₂ (Supplementary Fig. 9a), but with slightly lower
292 sensitivities. Therefore, our predictions of the GSL shifts based on all of the 880 cities
293 may be slightly overestimated with a rate of about 0.8–1.2 days·decade⁻¹ (Supplementary
294 Fig. 9b). Moreover, to verify the robustness of our analysis, we further calculated the
295 phenological differences between the 10-km and 30-km rural buffers and related them
296 with temperature and CO₂ gradients. Results from the gradients between 10-km and
297 30-km rural buffers showed higher correlations with temperature and CO₂ gradients than
298 those from the original urban–rural gradients (Supplementary Fig. 10). These higher
299 correlations not only confirm the robustness of our analysis, but also suggest that the

300 confounding factors (e.g., vegetation species, irrigation and nutrient supply) do not affect
301 the controlling role of temperature and CO₂ in vegetation photosynthetic phenology,
302 given that the vegetation phenology in 10-km rural buffers are less influenced by these
303 factors than urban areas. However, these confounding factors can hardly be included in
304 our analysis due to the lack of high-resolution data at global scale.

305 The novel insights of this study are derived at large scale from the contrasting
306 behaviour of plants along the urban–rural gradients. The sharp differences in
307 environmental conditions along these gradients can represent a unique “natural laboratory”
308 with different atmospheric CO₂ concentration and temperature that may ultimately inform
309 on plant behaviours under future climates and atmospheric composition. The
310 macro-environmental conditions of open urban laboratories are widely reachable in the
311 globe and can therefore lead to more general and robust assessments of vegetation
312 responses to key environmental drivers across different environmental conditions in a
313 global change perspective. Ultimately, our findings shed new light on the behaviour of
314 plants under global change, help to reduce the uncertainties of terrestrial ecosystems
315 models⁷⁴, and increase our understanding of climate–vegetation interactions.

316

317 **Methods**

318 *Urban–rural gradients*

319 We focused our study on urban clusters and their adjacent rural buffers at mid- to
320 high-latitudes in the Northern Hemisphere (NH, $\geq 30^\circ$) from 2015 to 2017
321 (Supplementary Fig. 1), where vegetation is highly seasonal and sensitive to climate^{61,66}.
322 The extents of the urban areas were mapped using a cluster-based method that estimates
323 optimal thresholds using nighttime stable-light data from the Defense Meteorological
324 Satellite Program/Operational Linescan System (DMSP/OLS)⁷⁵. Sensitivity analyses and
325 comparisons with other global urban-area products indicated that this product is reliable
326 and highly accurate⁷⁶. We used this data product (for 2013) instead of extracting urban
327 areas from land-cover data sets, because these cluster-based urban extents clearly define
328 the boundaries between urban and rural areas, regardless of the internal spatial
329 heterogeneity, which is more similar to the real environment than the vegetation
330 experiences. Although the static urban clusters (2013) and our study period (2015–2017)
331 differed by approximately three years, the overall results should not be affected due to
332 almost stable urban clusters in North America and Europe⁴¹ and the slightly increasing
333 urban areas in Asia⁷⁷.

334 We created a series of buffers extending 10, 20, 30 and 40 km outward from each
335 urban cluster perimeter to select an appropriate threshold for SIF data. Because of the
336 limited spatial coverage of the OCO-2 SIF data, we used an interval of 10 km to ensure
337 that each buffer had a sufficient number of observations. An example of the urban cluster

338 and its corresponding rural buffers was shown in [Supplementary Fig. 11](#). Pixels that were
339 water body or crops were excluded from this analysis ([Supplementary Fig. 11a](#)).
340 Croplands were excluded because their photosynthetic dynamics are strongly affected by
341 human management. We also excluded the pixels in the rural areas which had elevations
342 greater than ± 50 m of the average elevation of urban pixels (for both SIF and EVI data,
343 [Supplementary Fig. 11b](#))²¹. Given that the number of OCO-2 SIF observations per year
344 was low, we opted for the use of SIF data in each urban cluster and its corresponding
345 rural buffers from 2015 to 2017 as one completed phenological cycle. OCO-2 Footprints
346 with viewing zenith angles (VZA) less than 20° in glint and target modes are used⁷⁸. We
347 selected urban clusters with at least eight SIF observations in both the urban cluster and
348 each corresponding buffer to ensure a successful calculation of phenology. This resulted
349 in a total of 880 urban clusters ([Supplementary Fig. 1](#)).

350 *Data*

351 We used the OCO-2 SIF Lite product (B8100) at 757 nm for 2015–2017. OCO-2 is a
352 sun-synchronous polar-orbit satellite launched in July 2014, with an altitude of 705 km
353 and a descending node at approximately 13:30 local time¹⁸. OCO-2 leads the “A-Train”
354 satellite constellation with a repeating cycle of approximately 16 days. The instrument
355 collects high-resolution radiance spectra in the O₂-A band (757–775 nm), which can be
356 used to retrieve fluorescence signals from vegetation. Retrievals based on the in-filling of
357 solar Fraunhofer lines in narrow spectral windows around 757 and 771 nm were
358 conducted using the singular vector decomposition method. The accuracy of single

359 measurements at 757 nm after a series of bias-correction and quality-control steps is
360 approximately 15-25% of the typical peak values of SIF¹⁸. However, because there are
361 dozens of single measurements in each urban cluster and the corresponding rural buffer,
362 most of the noise in the retrieved SIF has been reduced following the $1/\sqrt{n}$ law, which
363 means the precision errors in the average of n samples will get reduced by a factor of
364 $1/\sqrt{n}$ ⁷⁹. Moreover, the relative uncertainties of single measurement in the urban clusters
365 and rural buffers are almost the identical (Supplementary Fig. 12); therefore, the retrieval
366 errors of SIF should have not large impacts on the urban–rural phenological patterns. We
367 chose the SIF data at 757 nm because the signals are approximately 1.5-fold greater at
368 757 than those at 771 nm.

369 The data for Aqua MODIS EVI collection-6 (MYD13A2; 16-day composite) with a
370 spatial resolution of 1 km for 2015–2017 were used to extract greenness phenology
371 information. The EVI data partially eliminate the effects of canopy background and
372 remain sensitive to small changes in vegetation activity compared to NDVI (normalized
373 vegetation index) data²⁰. Thus, the EVI data are considered to be more appropriate for use
374 in areas with sparse vegetation coverage, such as urban clusters^{21,38}. We used the Aqua
375 EVI data to maintain consistency with the OCO-2 overpass time (both occur at
376 approximately 13:30 local time). To make a comparison, the MODIS EVI data are
377 selected according to the same OCO-2 overpasses. To test whether the observed
378 urban–rural phenological patterns is an artefact of the difference in spatial resolutions
379 between OCO-2 SIF and MODIS EVI, we firstly resampled both SIF and EVI data to a

380 spatial resolution of 5 km and reproduced the urban–rural phenological differences. The
381 results also demonstrated larger differences of photosynthetic phenology in urban–rural
382 gradients than the differences of greenness phenology (Supplementary Fig. 5) and thus
383 demonstrated the robustness of our analysis.

384 We obtained the urban–rural XCO₂ gradients using reprocessed Lite files from the
385 OCO-2 product (version 8r) for 2015–2017. The data were bias-corrected using
386 observations from the Total Carbon Column Observing Network (TCCON). OCO-2 also
387 collects high-resolution radiance spectra at the 1.61 and 2.06 μm bands, except for the
388 O₂-A band, which can be used to retrieve XCO₂⁸⁰ based on the Atmospheric CO₂
389 Observations from Space algorithm. Comparisons with the measurements at TCCON
390 sites demonstrated that the precision of the Lite products was approximately 1.5 ppm⁸¹.

391 We used the Aqua MODIS collection-6 land-surface temperature (LST) data set
392 (MYD11A2; 8-day composite), with a spatial resolution of 1 km for 2015–2017 to
393 calculate the urban–rural LST gradient. We chose LST data from the Aqua satellite
394 because its data were acquired at 13:30 and 01:30 local time each day, approximately
395 representing the diurnal and nocturnal temperatures, respectively (i.e., maximum and
396 minimum temperatures). We also used the air surface temperature (AST) data from
397 TerraClimate dataset⁸², with a spatial resolution of 4 km to calculate the urban–rural AST
398 gradient.

399 We also extracted the mean annual air temperature (2 m above the surface) for each
400 urban cluster from the analytical data set based on both the Global Historical Climatology

401 Network (version 2) and the Climate Anomaly Monitoring System (GHCN-CAMS), with
402 a spatial resolution of 0.5°. The annual precipitation of each urban area was calculated
403 based on the monthly Integrated Multi-satellite Retrievals (IMERG) data set from global
404 precipitation measurements (GPMs), with a spatial resolution of 0.1°. Digital elevation
405 models (DEMs) at a spatial resolution of 30 arc seconds from the GTOPO30 data set and
406 the land-cover data set for 2015 from the European Space Agency (ESA) Climate Change
407 Initiative were also used in this study. We also used the global gridded nitrogen dioxide
408 (NO₂) and ozone (O₃) observations from Ozone Monitoring Instrument (OMI). We
409 calculated the mean LST changes for 2015–2035 at mid- to high-latitudes in the NH
410 ($\geq 30^\circ$) from four Earth system models (CSIRO-Mk3.6.0⁸³, GFDL-CM3⁸⁴, GISS-E2-H⁸⁵
411 and NorESM1-M⁸⁶) within CMIP5. Projected CO₂ concentration changes from 2015
412 were obtained from the RCP Database. Detailed information on the data sets is presented
413 in [Supplementary Table 1](#).

414 *Extraction of phenological data*

415 We used a double-sigmoidal function to fit the annual cycles of the SIF and EVI
416 observations⁸⁷. Choosing an appropriate method to fit noisy SIF data is important because
417 of the wide variation in phenology when estimated with different methods. We chose the
418 double-sigmoidal method for three reasons. First, the speeds of spring leaf out and
419 autumn senescence are not always the same: leaf out is generally faster than senescence⁸⁸.
420 The double-sigmoidal method can identify the actual biophysical dynamics of vegetation
421 by setting two amplitudes for spring and autumn⁸⁷. Second, functional fitting methods

422 have advantages for estimating phenology with noisy data⁸⁹. The OCO-2 data are
 423 acquired at different time intervals and are relatively noisy, and the number of
 424 observations is small. Thus some fitting approaches, such as polynomial fitting, logistic
 425 fitting and harmonic analysis, cannot be used or cannot converge to the global optimum.
 426 Third, the double-sigmoidal method has been successfully applied to SIF data in a
 427 previous study³³. The fitting equation is^{56,87}:

$$428 \quad y(t) = a_1 + \frac{a_2}{1 + \exp(-d_1(t - b_1))} - \frac{a_3}{1 + \exp(-d_2(t - b_2))} \quad (1)$$

429 where $y(t)$ represents the observed SIF or EVI for a given day of year (DOY; t); a_1
 430 represents the value in the winter dormant period; a_2 represents the value at the spring
 431 and early summer plateau; a_3 represents the value at the late summer and autumn plateau;
 432 b_1 and b_2 are the DOY mid-points of transitions for spring leaf out and autumn
 433 senescence, respectively; and d_1 and d_2 are the corresponding slope coefficients of these
 434 transitions.

435 The fitting equation was adapted to our SIF and EVI time series, and the coefficients
 436 were optimized using genetic algorithms. A simple weighting scheme was applied to the
 437 noisy data. We assigned a weight of two if a central point was within $\pm 50\%$ of the median
 438 for a moving window of three points³³. A maximum of 20 fitting attempts with different
 439 initial values were made until the fitting procedure converged to the global optimum.
 440 Each attempt had a maximum of 2000 iterations. The R^2 values of SIF fitting were lower
 441 than those of EVI, but most were larger than 0.8 (Supplementary Fig. 13). The R^2 values
 442 were generally high for the EVI data. The phenological indicators were then determined

443 using⁵⁶:

$$\begin{aligned}SOS &= b_1 - \frac{4.562}{2d_1} \\444 \quad POS &= 1.317 \left(-\left| \frac{1}{a_1} \right| + b_1 \right) \\EOS &= b_2 + \frac{4.562}{2d_2} \\GSL &= EOS - SOS\end{aligned} \quad (2)$$

445 where SOS, POS, EOS and GSL represent the start, peak, end and length of the growing
446 season, respectively. An example of the fitting method and the estimation of phenological
447 indicators is shown in [Supplementary Fig. S14a](#). We excluded some extreme values using
448 a loose threshold to reduce uncertainties and slightly adjusted the thresholds based on
449 previous studies [21,38,41](#) due to the differences between the data and methods. SOSs earlier
450 than the 30th or later than the 180th DOY, and EOSs earlier than the 240th or later than the
451 350th DOY, were thus excluded from our analysis. To test whether our results were
452 affected by the weighting scheme, we also calculated the phenological indicators after
453 changing the moving-window and without using the weighting scheme. Results showed
454 no significant differences compared to the original method ([Supplementary Fig. S14 b-c](#)).
455 The urban–rural phenological gradients were also evident using these different weighting
456 schemes ([Supplementary Fig. S14 d-e](#)).

457 *Conversion of urban–rural XCO₂ gradients to surface CO₂ gradients*

458 The XCO₂ data are column-averaged CO₂ mixed ratios and differ in magnitude from
459 CO₂ concentrations near the surface. Therefore, in order to investigate the effect of CO₂

460 fertilization on vegetation phenology, we need to convert the urban–rural XCO₂ gradients
461 to surface CO₂ gradients. Although atmospheric transport models would be the ideal
462 approach to fulfill this purpose, there are still many precluding issues. Firstly, high-spatial
463 resolution prior fluxes of CO₂, including the anthropogenic emissions and terrestrial
464 carbon uptake, as well as the high-resolution meteorological data (wind speed and wind
465 direction), still have large uncertainties, especially in urban areas with high-variable
466 emission sources (such as traffic pollution) and high degrees of surface heterogeneity^{90,91}.
467 Secondly, as one of the main factors that affect the variations of surface CO₂
468 concentration in finer scales, the heterogeneity of vertical profile in urban areas induced
469 by buildings can hardly be accurately estimated and illustrated⁹². Thirdly, continuous
470 high-spatiotemporal ground and satellite CO₂ measurements are still insufficient to
471 provide accurate constraints and evaluations for atmospheric transport models to simulate
472 the high-spatial resolution surface CO₂ concentrations at large scales⁹³. Therefore, global
473 near-surface CO₂ concentrations from atmospheric transport models or flux-inversion
474 systems generally have relatively low spatial resolutions⁹⁴, which cannot meet our needs
475 for deriving urban–rural gradients at large scales. Statistical methods are therefore more
476 appropriate for converting XCO₂ gradients to surface CO₂ gradients.

477 We used two approaches to determine the conversion factors. First, we used a
478 near-surface CO₂ data set with a comprehensive spatial coverage. The data were obtained
479 in Shanghai during April and May of 2014 and covered the entire urban area, with a total
480 of 172 sample points⁹⁵ (Supplementary Fig. 15). The slopes of the near-surface CO₂

481 measurements and OCO-2 XCO₂ observations in the same city were calculated
482 (Supplementary Fig. 16a-b). The conversion factor could then be obtained (K = 21.2).
483 Second, we collected a number of urban–rural surface CO₂ gradients from previous
484 studies (Supplementary Table 2) and then calculated the XCO₂ gradients of these urban
485 clusters and compared them via linear regression (Supplementary Fig. 16c), which
486 indicated that the conversion factor was approximately 28.5. These data from previous
487 literatures have an average of seven years gap with the satellite observations, and thus the
488 observations of urban–rural surface CO₂ gradients may be lower than those of present,
489 which possibly leads to a higher estimation of the K factor. Therefore, we used a K factor
490 of 25, which is the average value of these two approaches. Then we converted the
491 urban–rural XCO₂ gradients to surface CO₂ gradients through this conversion factor. This
492 conversion factor was derived via statistical methods that may have some uncertainties.
493 For example, the K factor derived from the first approach was 21.2 ± 8.3 ; while that from
494 the second approach was 28.5 ± 9.5 (mean \pm standard error). To test the robustness of our
495 results according to different K values, we repeated our analysis using a wide range of K
496 factors (from 19 to 30), which was the intersection of ranges of the K factors estimated
497 from these two approaches. Results showed that the partial correlations between
498 urban–rural phenological gradients and CO₂ gradients were not affected by K values,
499 given that this conversion factor was linear (Supplement Fig. 17a). Although the
500 predicted GSL had a declining trend when the K was increasing (Supplement Fig. 17b),
501 our predicted GSL shifts ($5.9\text{--}11.4$ days·decade⁻¹) based on a K factor of 25 were

502 comparable to the average value of these shifts. These results suggested that the joint
503 control of elevated CO₂ and temperature on urban–rural photosynthetic phenological
504 gradients was robust across different K values.

505 *Analysis*

506 The phenological differences, LST gradients and CO₂ gradients between urban and
507 rural areas for each city were first calculated as:

$$508 \quad \Delta P = P_{urban} - P_{rural} \quad (3)$$

509 where ΔP represents the urban–rural gradients for the phenological indicators (SOS, POS,
510 EOS and GSL), LST and CO₂ concentration; and P_{urban} and P_{rural} represent these values in
511 urban clusters and their corresponding rural buffers, respectively. The LST differences
512 included the mean spring LST (January to May, corresponding to SOS), mean summer
513 LST (June to August, corresponding to POS), mean autumn and winter LST (September
514 to December, corresponding to EOS) and mean annual LST (corresponding to GSL)³⁸.

515 Due to the limited OCO-2 observations, we used the whole year XCO₂ observations and
516 the conversion factor (K) to derive the urban–rural CO₂ gradients. The differences in
517 photosynthetic (SIF) and greenness (EVI) phenology along the urban–rural gradients for
518 different rural buffers (i.e., 10, 20, 30 and 40 km) were calculated ([Supplementary Fig. 4](#)).

519 Previous studies have shown that the mean footprint of urban areas on phenology was
520 about 20–25 km, which should be able to reflect the background vegetation
521 phenology^{21,38,96}. In this analysis, we found that the largest urban–rural phenological
522 differences occurred between urban clusters and 30-km rural buffers. Therefore, we

523 therefore used the 30-km rural buffers as representatives in the subsequent analyses.

524 The spatial distribution of photosynthetic phenology differences based on latitude,
525 mean annual air temperature and precipitation were then analysed. We also analysed the
526 phenological differences in different climate zones based on the Köppen–Geiger climate
527 zones classification (<http://people.eng.unimelb.edu.au/mpeel/koppen.html>). To determine
528 the main controlling drivers of urban–rural phenological gradients, we determined the
529 partial correlations of ΔP with latitude, longitude, urban size, mean annual air
530 temperature, annual precipitation, CO₂ gradient (ΔCO_2) and LST gradient (ΔLST). The
531 partial correlation (two-tailed) of each factor was determined while controlling the other
532 factors. In order to reduce the stochastic error, the LST and CO₂ gradients are binned
533 every 0.15°C and 1.5 ppm, respectively. Then we determined the main factors controlling
534 each phenological indicator by analysing the associations between urban–rural
535 phenological gradients with temperature and CO₂ enhancements. Furthermore, we
536 derived their sensitivities with a forward stepwise regression model ([Supplementary](#)
537 [Table 3](#)). This method automatically repeats the procedures of forward selection and
538 backward elimination. In each step, an explanatory variable is considered to either add or
539 subtract from the set of variables based on a sequence of F tests. Finally, we estimated the
540 near-term projected shifts in photosynthetic phenology by multiplying the sensitivities
541 with LST and CO₂ concentration predictions during 2015–2035 based on four RCP
542 scenarios (RCP 2.6, 4.5, 6.0 and 8.5).

543 Finally, we analysed the uncertainty of projected phenophase shifts as a consequence

544 of using LST other than air surface temperature (AST) to characterise the urban–rural
545 temperature gradients. Vegetation phenology theoretically should respond to AST more
546 than to LST. As shown in previous studies on the impact of land cover on temperature⁹⁷,
547 the spatial gradients of AST are likely smaller than that of LST (Supplementary Fig. 18a),
548 which may translate in a higher sensitivity of GSL to AST than to LST (Supplementary
549 Fig. 18b). Therefore, projected shifts of GSL based on urban–rural AST gradients might
550 be larger than that based on LST gradients (Supplementary Fig. 18c; approximately
551 0.5–0.8 days·decade⁻¹). However, current high-resolution AST datasets are generally
552 based on observations from weather stations, which cannot fully capture the small scale
553 urban–rural heterogeneity because of the low density of stations. Due to the limitation in
554 the current AST datasets, analysis based on this latter variable may actually have larger
555 uncertainties than those based on LST and will need more investigations in the future.

556 *Code availability*

557 The codes used to estimate the phenological indicators in this study are available at
558 https://drive.google.com/drive/folders/1yzcoRAjjubiLDqIlg6zbLUCfE_m1mHAsL?usp=s
559 [haring](#).

560 *Data availability*

561 OCO-2 SIF and XCO₂ data are available at <https://disc.gsfc.nasa.gov/>. MODIS EVI
562 and LST data are available at <https://ladsweb.modaps.eosdis.nasa.gov/>. Precipitation data
563 can be obtained from <https://pmm.nasa.gov>. GHCN-CAMS air temperature data are
564 available at <https://www.esrl.noaa.gov>. CCI Land cover data are available at

565 <http://maps.elie.ucl.ac.be/CCI/viewer/download.php>. GTOPO30 DEM data are available
566 at <https://earthexplorer.usgs.gov/>. NO₂ and O₃ data are available at
567 <http://www.temis.nl/index.php>. Projected CO₂ concentrations can be obtained from the
568 RCP Database (<http://www.iiasa.ac.at/web-apps/tnt/RcpDb>). Model results and the urban
569 clusters are available at
570 https://drive.google.com/drive/folders/1yzcoRAjjubiLDqIg6zbLUCfE_m1mHAsL?usp=s
571 [haring](#).

572 **References**

- 573 1 Canadell, J. G. *et al.* Contributions to accelerating atmospheric CO₂ growth from
574 economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of*
575 *the national academy of sciences* **104**, 18866-18870 (2007).
- 576 2 Keenan, T. F. *et al.* Net carbon uptake has increased through warming-induced
577 changes in temperate forest phenology. *Nature Climate Change* **4**, 598 (2014).
- 578 3 Peñuelas, J. & Filella, I. Phenology feedbacks on climate change. *Science* **324**,
579 887-888 (2009).
- 580 4 Richardson, A. D. *et al.* Climate change, phenology, and phenological control of
581 vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*
582 **169**, 156-173 (2013).
- 583 5 Richardson, A. D. *et al.* Ecosystem warming extends vegetation activity but
584 heightens vulnerability to cold temperatures. *Nature*,
585 doi:10.1038/s41586-018-0399-1 (2018).

- 586 6 Peñuelas, J. & Filella, I. Responses to a warming world. *Science* **294**, 793-795
587 (2001).
- 588 7 Piao, S. *et al.* Net carbon dioxide losses of northern ecosystems in response to
589 autumn warming. *Nature* **451**, 49 (2008).
- 590 8 Piao, S. *et al.* Leaf onset in the northern hemisphere triggered by daytime
591 temperature. *Nature communications* **6**, 6911 (2015).
- 592 9 Fu, Y. H. *et al.* Declining global warming effects on the phenology of spring leaf
593 unfolding. *Nature* **526**, 104-107 (2015).
- 594 10 IPCC. *Climate change 2014: synthesis report. Contribution of Working Groups I,
595 II and III to the fifth assessment report of the Intergovernmental Panel on Climate
596 Change.* (IPCC, 2014).
- 597 11 Calfapietra, C. *et al.* Challenges in elevated CO₂ experiments on forests. *Trends in
598 plant science* **15**, 5-10 (2010).
- 599 12 Fu, Y. H. *et al.* Larger temperature response of autumn leaf senescence than spring
600 leaf - out phenology. *Global change biology* (2017).
- 601 13 Wolkovich, E. M. *et al.* Warming experiments underpredict plant phenological
602 responses to climate change. *Nature* **485**, 494 (2012).
- 603 14 Calfapietra, C., Peñuelas, J. & Niinemets, Ü. Urban plant physiology:
604 adaptation-mitigation strategies under permanent stress. *Trends in plant science*
605 **20**, 72-75 (2015).
- 606 15 Peng, S. *et al.* Surface urban heat island across 419 global big cities.

- 607 *Environmental science & technology* **46**, 696-703 (2011).
- 608 16 Schwandner, F. M. *et al.* Spaceborne detection of localized carbon dioxide
609 sources. *Science* **358**, eaam5782 (2017).
- 610 17 Zhao, S., Liu, S. & Zhou, D. Prevalent vegetation growth enhancement in urban
611 environment. *Proceedings of the National Academy of Sciences* **113**, 6313-6318,
612 doi:10.1073/pnas.1602312113 (2016).
- 613 18 Sun, Y. *et al.* Overview of Solar-Induced chlorophyll Fluorescence (SIF) from the
614 Orbiting Carbon Observatory-2: Retrieval, cross-mission comparison, and global
615 monitoring for GPP. *Remote Sensing of Environment* **209**, 808-823 (2018).
- 616 19 Guanter, L. *et al.* Global and time-resolved monitoring of crop photosynthesis
617 with chlorophyll fluorescence. *Proceedings of the National Academy of Sciences*
618 **111**, E1327-E1333 (2014).
- 619 20 Huete, A. *et al.* Overview of the radiometric and biophysical performance of the
620 MODIS vegetation indices. *Remote sensing of environment* **83**, 195-213 (2002).
- 621 21 Zhou, D., Zhao, S., Zhang, L. & Liu, S. Remotely sensed assessment of
622 urbanization effects on vegetation phenology in China's 32 major cities. *Remote*
623 *Sensing of Environment* **176**, 272-281 (2016).
- 624 22 Zhou, D., Zhao, S., Liu, S., Zhang, L. & Zhu, C. Surface urban heat island in
625 China's 32 major cities: Spatial patterns and drivers. *Remote Sensing of*
626 *Environment* **152**, 51-61 (2014).
- 627 23 Chuine, I., Morin, X. & Bugmann, H. Warming, photoperiods, and tree phenology.

- 628 *Science* **329**, 277-278 (2010).
- 629 24 Fu, Y. H., Campioli, M., Deckmyn, G. & Janssens, I. A. Sensitivity of leaf
630 unfolding to experimental warming in three temperate tree species. *Agricultural
631 and Forest Meteorology* **181**, 125-132 (2013).
- 632 25 Jeong, S.-J. *et al.* Application of satellite solar-induced chlorophyll fluorescence
633 to understanding large-scale variations in vegetation phenology and function over
634 northern high latitude forests. *Remote sensing of environment* **190**, 178-187
635 (2017).
- 636 26 Kikuzawa, K. Phenological and morphological adaptations to the light
637 environment in two woody and two herbaceous plant species. *Functional Ecology*
638 **17**, 29-38 (2003).
- 639 27 Daumard, F. *et al.* A field platform for continuous measurement of canopy
640 fluorescence. *IEEE Transactions on geoscience and Remote Sensing* **48**,
641 3358-3368 (2010).
- 642 28 Suni, T. *et al.* Interannual variability and timing of growing - season CO₂
643 exchange in a boreal forest. *Journal of Geophysical Research: Atmospheres* **108**
644 (2003).
- 645 29 Medvigy, D., Jeong, S. J., Clark, K. L., Skowronski, N. S. & Schäfer, K. V.
646 Effects of seasonal variation of photosynthetic capacity on the carbon fluxes of a
647 temperate deciduous forest. *Journal of Geophysical Research: Biogeosciences*
648 **118**, 1703-1714 (2013).

- 649 30 Chen, X., Wang, D., Chen, J., Wang, C. & Shen, M. The mixed pixel effect in
650 land surface phenology: A simulation study. *Remote Sensing of Environment* **211**,
651 338-344 (2018).
- 652 31 Filella, I., Penuelas, J., Llorens, L. & Estiarte, M. Reflectance assessment of
653 seasonal and annual changes in biomass and CO₂ uptake of a Mediterranean
654 shrubland submitted to experimental warming and drought. *Remote Sensing of*
655 *Environment* **90**, 308-318 (2004).
- 656 32 Hilker, T. *et al.* Remote sensing of photosynthetic light-use efficiency across two
657 forested biomes: Spatial scaling. *Remote Sensing of Environment* **114**, 2863-2874
658 (2010).
- 659 33 Walther, S. *et al.* Satellite chlorophyll fluorescence measurements reveal large -
660 scale decoupling of photosynthesis and greenness dynamics in boreal evergreen
661 forests. *Global change biology* **22**, 2979-2996 (2016).
- 662 34 Porcar-Castell, A. *et al.* Linking chlorophyll a fluorescence to photosynthesis for
663 remote sensing applications: mechanisms and challenges. *Journal of experimental*
664 *botany* **65**, 4065-4095 (2014).
- 665 35 Baker, N. R. Chlorophyll fluorescence: a probe of photosynthesis in vivo. *Annu.*
666 *Rev. Plant Biol.* **59**, 89-113 (2008).
- 667 36 Norton Alexander, J., Rayner Peter, J. & Koffi Ernest, N. Assimilating
668 solar-induced chlorophyll fluorescence into the terrestrial biosphere model
669 BETHY-SCOPE: Model description and information content. 1-26 (2017).

- 670 37 White, M. A., Nemani, R. R., Thornton, P. E. & Running, S. W. Satellite evidence
671 of phenological differences between urbanized and rural areas of the eastern
672 United States deciduous broadleaf forest. *Ecosystems* **5**, 260-273 (2002).
- 673 38 Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H. & Schneider, A. The
674 footprint of urban climates on vegetation phenology. *Geophysical Research*
675 *Letters* **31** (2004).
- 676 39 Han, G. & Xu, J. Land surface phenology and land surface temperature changes
677 along an urban–rural gradient in Yangtze River Delta, China. *Environmental*
678 *management* **52**, 234-249 (2013).
- 679 40 Cong, N. *et al.* Spring vegetation green-up date in China inferred from SPOT
680 NDVI data: A multiple model analysis. *Agricultural and Forest Meteorology* **165**,
681 104-113 (2012).
- 682 41 Li, X. *et al.* Response of vegetation phenology to urbanization in the
683 conterminous United States. *Global change biology* **23**, 2818-2830 (2017).
- 684 42 Niu, S. *et al.* Seasonal hysteresis of net ecosystem exchange in response to
685 temperature change: patterns and causes. *Global Change Biology* **17**, 3102-3114
686 (2011).
- 687 43 Van der Tol, C., Verhoef, W. & Rosema, A. A model for chlorophyll fluorescence
688 and photosynthesis at leaf scale. *Agricultural and forest meteorology* **149**, 96-105
689 (2009).
- 690 44 Sun, Y. *et al.* OCO-2 advances photosynthesis observation from space via

691 solar-induced chlorophyll fluorescence. *Science* **358**, eaam5747 (2017).

692 45 Zarco-Tejada, P., Morales, A., Testi, L. & Villalobos, F. Spatio-temporal patterns
693 of chlorophyll fluorescence and physiological and structural indices acquired
694 from hyperspectral imagery as compared with carbon fluxes measured with eddy
695 covariance. *Remote Sensing of Environment* **133**, 102-115 (2013).

696 46 Yang, X. *et al.* Solar - induced chlorophyll fluorescence that correlates with
697 canopy photosynthesis on diurnal and seasonal scales in a temperate deciduous
698 forest. *Geophysical Research Letters* **42**, 2977-2987 (2015).

699 47 Joiner, J. *et al.* The seasonal cycle of satellite chlorophyll fluorescence
700 observations and its relationship to vegetation phenology and ecosystem
701 atmosphere carbon exchange. *Remote Sensing of Environment* **152**, 375-391
702 (2014).

703 48 CaraDonna, P. J., Iler, A. M. & Inouye, D. W. Shifts in flowering phenology
704 reshape a subalpine plant community. *Proceedings of the National Academy of
705 Sciences* **111**, 4916-4921 (2014).

706 49 Menzel, A. *et al.* European phenological response to climate change matches the
707 warming pattern. *Global change biology* **12**, 1969-1976 (2006).

708 50 Thompson, R. & Clark, R. Is spring starting earlier? *The Holocene* **18**, 95-104
709 (2008).

710 51 Miller-Rushing, A. J. & Primack, R. B. Global warming and flowering times in
711 Thoreau's Concord: a community perspective. *Ecology* **89**, 332-341 (2008).

- 712 52 Vitasse, Y. *et al.* Leaf phenology sensitivity to temperature in European trees: Do
713 within-species populations exhibit similar responses? *Agricultural and forest*
714 *meteorology* **149**, 735-744 (2009).
- 715 53 Piao, S. *et al.* Weakening temperature control on the interannual variations of
716 spring carbon uptake across northern lands. *Nature Climate Change* **7**, 359
717 (2017).
- 718 54 Körner, C. & Basler, D. Phenology under global warming. *Science* **327**,
719 1461-1462 (2010).
- 720 55 Way, D. A. & Montgomery, R. A. Photoperiod constraints on tree phenology,
721 performance and migration in a warming world. *Plant, Cell & Environment* **38**,
722 1725-1736 (2015).
- 723 56 Gonsamo, A., Chen, J. M. & Ooi, Y. W. Peak season plant activity shift towards
724 spring is reflected by increasing carbon uptake by extratropical ecosystems.
725 *Global change biology* (2017).
- 726 57 Xu, C., Liu, H., Williams, A. P., Yin, Y. & Wu, X. Trends toward an earlier peak
727 of the growing season in Northern Hemisphere mid - latitudes. *Global change*
728 *biology* **22**, 2852-2860 (2016).
- 729 58 Wu, C. *et al.* Contrasting responses of autumn-leaf senescence to daytime and
730 night-time warming. *Nature Climate Change*, 1 (2018).
- 731 59 Marchin, R. M., Salk, C. F., Hoffmann, W. A. & Dunn, R. R. Temperature alone
732 does not explain phenological variation of diverse temperate plants under

733 experimental warming. *Global change biology* **21**, 3138-3151 (2015).

734 60 Sigurdsson, B. D. Elevated CO₂ and nutrient status modified leaf phenology and
735 growth rhythm of young *Populus trichocarpa* trees in a 3-year field study. *Trees*
736 **15**, 403-413 (2001).

737 61 Liu, Q. *et al.* Delayed autumn phenology in the Northern Hemisphere is related to
738 change in both climate and spring phenology. *Global change biology* **22**,
739 3702-3711 (2016).

740 62 Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A. & Field, C. B.
741 Diverse responses of phenology to global changes in a grassland ecosystem.
742 *Proceedings of the National Academy of Sciences* **103**, 13740-13744 (2006).

743 63 Jach, M. E. & Ceulemans, R. Effects of elevated atmospheric CO₂ on phenology,
744 growth and crown structure of Scots pine (*Pinus sylvestris*) seedlings after two
745 years of exposure in the field. *Tree physiology* **19**, 289-300 (1999).

746 64 Taylor, G. *et al.* Future atmospheric CO₂ leads to delayed autumnal senescence.
747 *Global Change Biology* **14**, 264-275 (2008).

748 65 NOAA National Centers for Environmental Information, State of the Climate:
749 Global Climate Report for May 2018, published online June 2018, retrieved on
750 June 24, 2018 from <https://www.ncdc.noaa.gov/sotc/global/201805>.

751 66 Jeong, S. J., HO, C. H., GIM, H. J. & Brown, M. E. Phenology shifts at start vs.
752 end of growing season in temperate vegetation over the Northern Hemisphere for
753 the period 1982–2008. *Global change biology* **17**, 2385-2399 (2011).

- 754 67 Barichivich, J. *et al.* Large - scale variations in the vegetation growing season and
755 annual cycle of atmospheric CO₂ at high northern latitudes from 1950 to 2011.
756 *Global change biology* **19**, 3167-3183 (2013).
- 757 68 Buyantuyev, A. & Wu, J. Urbanization diversifies land surface phenology in arid
758 environments: interactions among vegetation, climatic variation, and land use
759 pattern in the Phoenix metropolitan region, USA. *Landscape and Urban Planning*
760 **105**, 149-159 (2012).
- 761 69 Decina, S. M., Templer, P. H. & Hutyra, L. R. Atmospheric Inputs of Nitrogen,
762 Carbon, and Phosphorus across an Urban Area: Unaccounted Fluxes and Canopy
763 Influences. *Earth's Future* **6**, 134-148 (2018).
- 764 70 Gregg, J. W., Jones, C. G. & Dawson, T. E. Urbanization effects on tree growth in
765 the vicinity of New York City. *Nature* **424**, 183 (2003).
- 766 71 Zhang, X., Friedl, M. A., Schaaf, C. B., Strahler, A. H. & Liu, Z. Monitoring the
767 response of vegetation phenology to precipitation in Africa by coupling MODIS
768 and TRMM instruments. *Journal of Geophysical Research: Atmospheres* **110**
769 (2005).
- 770 72 Do, F. C. *et al.* Environmental influence on canopy phenology in the dry tropics.
771 *Forest Ecology and Management* **215**, 319-328 (2005).
- 772 73 Peñuelas, J. *et al.* Complex spatiotemporal phenological shifts as a response to
773 rainfall changes. *New Phytologist* **161**, 837-846 (2004).
- 774 74 Fisher, J. B., Huntzinger, D. N., Schwalm, C. R. & Sitch, S. Modeling the

775 terrestrial biosphere. *Annual Review of Environment and Resources* **39**, 91-123
776 (2014).

777 75 Zhou, Y. *et al.* A cluster-based method to map urban area from DMSP/OLS
778 nightlights. *Remote Sensing of Environment* **147**, 173-185 (2014).

779 76 Zhou, Y. *et al.* A global map of urban extent from nightlights. *Environmental*
780 *Research Letters* **10**, 054011 (2015).

781 77 Huang, X., Schneider, A. & Friedl, M. A. Mapping sub-pixel urban expansion in
782 China using MODIS and DMSP/OLS nighttime lights. *Remote Sensing of*
783 *Environment* **175**, 92-108 (2016).

784 78 Zhang, Y. *et al.* On the relationship between sub-daily instantaneous and daily
785 total gross primary production: Implications for interpreting satellite-based SIF
786 retrievals. *Remote Sensing of Environment* **205**, 276-289,
787 doi:10.1016/j.rse.2017.12.009 (2018).

788 79 Frankenberg, C. *et al.* Prospects for chlorophyll fluorescence remote sensing from
789 the Orbiting Carbon Observatory-2. *Remote Sensing of Environment* **147**, 1-12
790 (2014).

791 80 Crisp, D. *et al.* The on-orbit performance of the Orbiting Carbon Observatory-2
792 (OCO-2) instrument and its radiometrically calibrated products. *Atmospheric*
793 *Measurement Techniques* **10**, 59 (2017).

794 81 Wunch, D. *et al.* Comparisons of the Orbiting Carbon Observatory-2 (OCO-2)
795 XCO₂ measurements with TCCON. *Atmospheric Measurement Techniques* **10**,

796 2209 (2017).

797 82 Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A. & Hegewisch, K. C.
798 TerraClimate, a high-resolution global dataset of monthly climate and climatic
799 water balance from 1958–2015. *Scientific data* **5**, 170191 (2018).

800 83 Collier, M. *et al.* in *International Congress on Modelling and*
801 *Simulation–MODSIM*.

802 84 Griffies, S. M. *et al.* The GFDL CM3 coupled climate model: characteristics of
803 the ocean and sea ice simulations. *Journal of Climate* **24**, 3520-3544 (2011).

804 85 Schmidt, G. A. *et al.* Configuration and assessment of the GISS ModelE2
805 contributions to the CMIP5 archive. *Journal of Advances in Modeling Earth*
806 *Systems* **6**, 141-184 (2014).

807 86 Bentsen, M. *et al.* The Norwegian earth system model, NorESM1-M—Part 1:
808 Description and basic evaluation of the physical climate. *Geosci. Model Dev* **6**,
809 687-720 (2013).

810 87 Gonsamo, A., Chen, J. M. & D’Odorico, P. Deriving land surface phenology
811 indicators from CO₂ eddy covariance measurements. *Ecological indicators* **29**,
812 203-207 (2013).

813 88 Elmore, A. J., Guinn, S. M., Minsley, B. J. & Richardson, A. D. Landscape
814 controls on the timing of spring, autumn, and growing season length in mid -
815 Atlantic forests. *Global Change Biology* **18**, 656-674 (2012).

816 89 Hird, J. N. & McDermid, G. J. Noise reduction of NDVI time series: An empirical

- 817 comparison of selected techniques. *Remote Sensing of Environment* **113**, 248-258
818 (2009).
- 819 90 Duren, R. M. & Miller, C. E. Measuring the carbon emissions of megacities.
820 *Nature Climate Change* **2**, 560 (2012).
- 821 91 Bréon, F. *et al.* An attempt at estimating Paris area CO₂ emissions from
822 atmospheric concentration measurements. *Atmospheric Chemistry and Physics* **15**,
823 1707-1724 (2015).
- 824 92 Chen, F. *et al.* The integrated WRF/urban modelling system: development,
825 evaluation, and applications to urban environmental problems. *International*
826 *Journal of Climatology* **31**, 273-288 (2011).
- 827 93 Chevallier, F. *et al.* Toward robust and consistent regional CO₂ flux estimates
828 from in situ and spaceborne measurements of atmospheric CO₂. *Geophysical*
829 *Research Letters* **41**, 1065-1070 (2014).
- 830 94 Peters, W. *et al.* An atmospheric perspective on North American carbon dioxide
831 exchange: CarbonTracker. *Proceedings of the National Academy of Sciences* **104**,
832 18925-18930 (2007).
- 833 95 Liu, M. *et al.* Spatial variation of near-surface CO₂ concentration during spring in
834 Shanghai. *Atmospheric Pollution Research* **7**, 31-39 (2016).
- 835 96 Zhou, D., Zhao, S., Zhang, L., Sun, G. & Liu, Y. The footprint of urban heat
836 island effect in China. *Scientific reports* **5**, 11160 (2015).
- 837 97 Alkama, R. & Cescatti, A. Biophysical climate impacts of recent changes in

838 global forest cover. *Science* **351**, 600-604, doi:10.1126/science.aac8083 (2016).

839

840

841 **Acknowledgements**

842 This research was financially supported by the National Key R&D Program of China
843 (2016YFA0600202), the Strategic Priority Research Program of the Chinese Academy of
844 Sciences under Grants XDA19040500, Jiangsu Provincial Natural Science Fund for
845 Distinguished Young Scholars of China (BK20170018), International Cooperation and
846 Exchange Programs between NSFC and DFG (41761134082) and General Program of
847 National Science Foundation of China (41671421). JP would like to acknowledge the
848 financial support from the European Research Council Synergy grant
849 ERC-SyG-2013-610028 IMBALANCE-P. AH acknowledges financial support from
850 Australian Research Council Discovery Program grant DP170101630. S.H.W was
851 supported by the Postgraduate Research & Practice Innovation Program of Jiangsu
852 Province (KYCX18_0037) and the Key Research Program of the Chinese Academy of
853 Sciences (Grant NO., KFZD-SW-310).

854 **Author contributions**

855 Y.G.Z. designed the research; S.H.W. performed the analysis; S.H.W., Y.G.Z. and W.M.J.
856 drafted the paper; J.P., and A.C. contributed to the interpretation of the results and to the
857 writing of the paper; A.H., Y.Y.Z. and Y.S.F. contributed to the writing of the paper; Y.Y.Z.
858 and M. L. provided the data.

859 **Competing interests**

860 The authors declare no competing interests.

861

862 **Fig. 1.** Mean urban–rural phenological differences based on SIF and EVI. SOS, start of
863 growing season; POS, peak of growing season; EOS, end of growing season; GSL, length
864 of growing season. The operator Δ represents the differences in phenological indicators
865 between urban areas and rural buffers (e.g., $\Delta\text{SOS} = \text{SOS}_{\text{urban}} - \text{SOS}_{\text{rural}}$). The error bars
866 represent standard errors of the mean ($n = 880$).

867 **Fig. 2.** Spatial distributions of ΔSOS (a), ΔPOS (b), ΔEOS (c) and ΔGSL (d) for SIF ($n =$
868 880). The first column represents the urban effects on phenological metrics for various
869 urban clusters. The second column represents phenological differences based on
870 latitudinal profiles (the shaded areas represent the standard errors of the mean); whereas
871 the third column shows the average metrics for various climatic backgrounds (mean
872 annual air temperature and annual precipitation).

873 **Fig. 3.** Partial correlations of SIF (a) and EVI (b) urban–rural phenological differences
874 (ΔSOS , ΔPOS , ΔEOS and ΔGSL) with explanatory variables. Lat: latitude; Lon: longitude;
875 Size: log 10 of the urban size; Air T: mean annual air temperature; Pre: mean annual
876 precipitation; ΔCO_2 : urban–rural CO_2 difference; $\Delta\text{T}_{\text{day}}$: daytime urban–rural land surface
877 temperature difference; $\Delta\text{T}_{\text{night}}$: night-time urban–rural land surface temperature difference;
878 SOS: start of growing season; POS: peak of growing season; EOS: end of growing season;
879 GSL: length of growing season. *: $p < 0.05$; **: $p < 0.01$ ($n = 880$).

880 **Fig. 4.** Associations between elevated temperature (a–d), CO_2 (e–h) and urban–rural
881 photosynthetic phenological gradients. ΔCO_2 , urban–rural CO_2 gradient; $\Delta\text{LST}_{\text{day}}$,
882 urban–rural gradient of daytime LST. The LST and CO_2 gradients are binned every

883 0.15°C and 1.5 ppm, respectively; each dot represents a bin. The solid lines indicate
884 significant trends and the shaded areas represent the 95% confidence intervals, and p
885 values represent the significance (Student's t -tests, $n = 880$).

886 **Fig. 5.** Projected shifts in photosynthetic phenology during the next two decades.
887 Sensitivities of photosynthetic phenology to temperature (a) and CO₂ (b). The error bars
888 represent standard errors of the mean. c–f, Shifts of photosynthetic SOS, POS, EOS and
889 GSL from 2015 to 2035, as calculated from the sensitivities shown in a–b and LST and
890 CO₂ concentration predictions during 2015–2035 from four “Representative
891 Concentration Pathway” (RCP) scenarios. The shaded areas represent the standard errors.
892 g, Projected shifts of photosynthetic phenology during the next two decades in per decade
893 (days·decade⁻¹). The negative values represent the advances of SOS and POS, and
894 positive values represent a delayed EOS and a prolonged GSL. The error bars represent
895 standard errors of the mean.









