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

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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/1yzcoRAjjubiLDqlg6zbLUCfE_m1mHAsL?usp=s
571 [haring](#).

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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.









