

1 Urban warming favours C₄ plants in temperate European cities

2

3 Grant A. Duffy*

4 School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

5 grant.duffy@monash.edu

6 +61 (0) 3 990 29913

7

8 Steven L. Chown

9 School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia

10 steven.chown@monash.edu

11

12 *Corresponding author

13

14 Running headline: Urban warming restructures plant assemblages

15 **Summary**

- 16 1) Elucidating the mechanisms responsible for the structure of urban
17 communities is a key aim of urban ecology, but one that is often confounded
18 by the multitude of environmental changes that are caused by urbanisation.
19 We applied trait-based techniques to identify the specific environmental
20 drivers that shape urban plant assemblages and predict how these drivers will
21 further impact biotas with increasing urbanisation and global environmental
22 change.
- 23 2) Urbanised areas across temperate Europe have significantly higher abundance
24 and richness of plants using the C₄ photosynthetic pathway, relative to the
25 total number and species richness of all plant records, than non-urban areas.
- 26 3) Urban warming, mediated by the contrasting physiological responses of C₃
27 and C₄ plants to warming, is the main driver of observed patterns of plant
28 assemblage structure. This mirrors broad-scale and historical distribution
29 patterns of C₃ and C₄ plants. The increased relative abundance of C₄ plants in
30 cities demonstrated here may be indicative of more geographically widespread
31 assemblage changes to be expected in temperate environments under
32 continuing global climate change.
- 33 4) *Synthesis*: Applying a combined trait-based, ecoinformatic and remote-sensing
34 approach provides new insight into the landscape-level consequences of
35 urbanisation. Specifically, we show that localised urban warming in cities
36 across temperate Europe favours C₄ plant species, which respond positively to
37 increased temperatures. Urban plant assemblages are shaped by environmental
38 warming and exhibit significant increases in C₄ plant relative abundance
39 compared to non-urban assemblages.

40

41 **Keywords:** ecophysiology, environmental change, macroecology, photosynthetic

42 pathway, plant–climate interactions, urban heat islands, urbanisation

43

44 **Introduction**

45 Urbanisation forms a key and growing modern environmental challenge. With an
46 increasing global population, and a rural-urban demographic shift, an ever-increasing
47 number of people live in urbanised areas (United Nations 2015). Urban land cover in
48 2030 is predicted to be three times the urban area observed in 2000 (Seto, Güneralp &
49 Hutryra 2012), and the ecological impacts of this urban expansion are expected to be
50 substantial and extensive (Grimm *et al.* 2008; Gaston, Davies & Edmondson 2010;
51 Aronson *et al.* 2014). At the same time, urbanisation, and the environmental changes
52 that it effects (Seto & Shepherd 2009), present a valuable opportunity to explore
53 fundamental questions in ecology. One such question is how organismal traits
54 mediate environmental variation to structure plant and animal communities (Diamond
55 *et al.* 2015; Hahs & Evans 2015; Williams, Hahs & Vesk 2015), a significant area of
56 current interest (e.g. Violle *et al.* 2014; Chown & Gaston 2016).

57

58 The urban heat island (UHI) effect is arguably one of the most pronounced and
59 ecologically significant climatic changes caused by urbanisation (Seto & Shepherd
60 2009; Gaston, Davies & Edmondson 2010). Modifications of the physical
61 environment (see Oke 1981; Seto & Shepherd 2009; Phelan *et al.* 2015) alter the
62 thermodynamics of an urban system, which generally leads to increases in ambient
63 temperature, relative to surrounding non-urban areas. The magnitude of, and area
64 affected by, this warming is the product of background climatic conditions,
65 population and area of a city, urban planning and cultural factors (Zhao *et al.* 2014).

66

67 Local climatic changes brought about by UHIs are expected to impact urban
68 communities through thermal niche filtering (Williams *et al.* 2009; Chown & Duffy

69 2015). Identifying the specific effects of altered climatic variables is, however,
70 confounded by the multitude of other environmental changes associated with
71 urbanisation (Seto & Shepherd 2009). Trait-based methods provide a means to
72 disentangle these confounding effects and identify the specific environmental drivers
73 that shape urban biotas (Williams, Hahs & Vesk 2015). Plants are an ideal group in
74 which to apply trait-based methods to understand the assemblage-level impacts of
75 UHIs due to the well-documented differences in the responses of the C₃ and C₄
76 photosynthetic pathways to temperature (e.g. Hattersley 1983; Sage & Kubien 2007;
77 Yamori, Hikosaka & Way 2013).

78

79 C₃ plants are more tolerant of, and better able to acclimate to, a broad range of
80 temperatures than their C₄ counterparts (Yamori, Hikosaka & Way 2013).

81 Photosynthetic activity increases rapidly in C₄ plants between 20 and 40 °C (Pearcy &
82 Ehleringer 1984) and, at higher temperatures (~ 40 ° C, dependent on [CO₂]), the
83 average photosynthetic rate of C₄ plants is more than double that of C₃ plants
84 (Yamori, Hikosaka & Way 2013). In their controlled plant-growth experiments,
85 Bijoor et al. (2008) noted that biomass of C₄ plants increased substantially in heated
86 plots, demonstrating that increased yield of C₄ photosynthesis under warmer
87 conditions is translated into gains in plant growth. These mechanisms provide a
88 compelling explanation for why ambient temperature has been identified as a key
89 determinant of patterns of C₃ and C₄ plant distributions and relative abundances
90 (Hattersley 1983; Ueno & Takeda 1992; Ehleringer, Cerling & Helliker 1997; Hanba,
91 Kobayashi & Enomoto 2009; Pyankov *et al.* 2010; Pau, Edwards & Still 2012;
92 Angelo & Daehler 2015). For example, C₄ plant species across Australian grasslands
93 increase in abundance with increasing temperature, while C₃ plants exhibit the

94 opposite response (Hattersley 1983). Similar geographic patterns have been identified
95 in European (Pyankov *et al.* 2010) and Japanese (Ueno & Takeda 1992; Hanba,
96 Kobayashi & Enomoto 2009) plant assemblages, and elevation gradients of C₃ and C₄
97 grasses in Hawai'i have also been attributed to environmental temperature (Angelo &
98 Daehler 2015).

99

100 The relatively low photosynthetic yields of C₄ photosynthesis under cool, wet
101 conditions (Sage & Kubien 2007), coupled with the poor freeze-tolerance of C₄ plants
102 (Osborne *et al.* 2008), mean that C₃ plants dominate plant assemblages across Europe.
103 C₄ plant species account for a small proportion of all plant species (0.51 – 1.50 %;
104 Collins & Jones 1985), or are altogether absent (Ehleringer, Cerling & Helliker 1997)
105 from temperate European assemblages. Urban heat islands may, however, sufficiently
106 alter the local climate such that C₄ plants in urban regions are more productive than
107 those in non-urban areas. Gains in photosynthetic yield (Pearcy & Ehleringer 1984;
108 Sage & Kubien 2007; Yamori, Hikosaka & Way 2013) and biomass (Bijoor *et al.*
109 2008) at higher temperatures should enable C₄ plants to have higher fitness, relative to
110 their C₃ counterparts, and could potentially restructure urban plant assemblages.
111 Indeed, it has been suggested that urban warming will favour C₄ plants (Duncan *et al.*
112 2011), though no explicit tests of the idea have been conducted. Here, we test the
113 hypothesis that UHI warming restructures plant assemblages and favours C₄ plants in
114 cities across temperate Europe. To do so, we combine trait data on photosynthetic
115 pathways, ecoinformatic approaches (Michener & Jones 2012) using data from the
116 Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>), and remotely-
117 sensed measurements of UHI warming.

118

119

120 **Material and methods**

121 The United Kingdom and Germany were selected as exemplar representatives of the
122 temperate European region, especially given climatic variation between the two
123 countries owing to their more oceanic and continental settings (Peel et al. 2007),
124 respectively. Both countries contain substantial urbanised areas and are extensively
125 sampled with a large number of botanical records in the Global Biodiversity
126 Information Facility (GBIF), which minimises the spatial bias often associated with
127 GBIF data (Yesson *et al.* 2007; Boakes *et al.* 2010). Georeferenced occurrence data
128 with ‘no known coordinate issues’ for all plant records in the UK
129 (doi:10.15468/dl.g4lis4; n = 20 477 246) and Germany (doi:10.15468/dl.misihs; n = 5
130 386 025) were downloaded from GBIF. Although the C₄ photosynthetic pathway only
131 occurs in angiosperms, all plants were included in subsequent analyses to present an
132 overview of changes to whole plant assemblages. Nevertheless, repeat analyses were
133 performed using only angiosperm records to rule out taxonomic bias.

134

135 Duplicate records were removed from both datasets and point data were cropped
136 using geographic boundary shapefiles. Counts of all plant occurrence data at a quarter
137 degree resolution (~ 19 km x 28 km) were made. Analyses using this relatively coarse
138 spatial resolution were necessary to compensate for coordinate rounding and minor
139 geositional errors of GBIF data. Any cell with fewer than 1000 unique points was
140 excluded from further analyses. Urban cells were identified using an urban area
141 shapefile derived from 500 m resolution MODIS data (Schneider, Friedl & Potere
142 2010), which was rasterised to 0.25 ° resolution. C₄ plants were identified using the
143 list of European C₄ plants compiled by Pyankov *et al.* (2010) and records from

144 GrassPortal (Osborne et al. 2014). Any plant identified as using the C₄ photosynthetic
145 pathway by either of these sources was accepted as a C₄ species for the purposes of
146 our analyses.

147

148 The relative abundance of plants using the C₄ photosynthesis pathway was calculated
149 by dividing the number of occurrences of species identified as C₄ plants by the total
150 number of occurrence records per 0.25° cell. Species richness of all plants and species
151 richness of C₄ plants was calculated by counting the unique instances of species in
152 each cell. The latter was divided by the former to calculate the species richness
153 contribution of C₄ plants. All resultant values were expressed as percentages (i.e.
154 multiplied by 100). Relative abundance and species richness contribution of C₄ plants
155 in urban and non-urban cells were compared using Mann-Whitney U tests.

156

157 The use of C₄ plant relative abundance from GBIF data as an approximation of
158 ecological abundance relies on the assumption that sampling and reporting of records
159 is not biased toward either C₃ or C₄ plants. Although direct bias in favour of either
160 photosynthetic pathway is unlikely, taxonomic bias may indirectly skew abundance
161 estimates. For example, as approximately 80% of known C₄ species are monocots
162 (Sage 2016), overrepresentation of this taxon in urban GBIF records may inflate the
163 relative abundance of C₄ species such that it is no longer a valid representation of
164 ecological abundances. To ensure that the results of the all-plants analyses were
165 robust to such taxonomic biases, analyses were repeated using monocot and eudicot
166 plant occurrence records separately.

167

168 To test if observed patterns of C₄ relative abundance were the result of biases arising
169 from sampling effort, a randomisation procedure was used to generate randomised C₄
170 proportion maps based on sampling effort for each quarter degree cell. Pooled species
171 records for each country were randomly redistributed amongst cells based on the
172 sampling effort for each cell (i.e. number of records per cell). From these randomised
173 data the C₄ plant proportion for each cell was calculated by dividing the number of
174 newly distributed records of C₄ plants by the total record count of each cell. This
175 randomisation procedure was replicated 999 times to generate randomised maps of
176 plant distribution based on sampling effort. Kolgorov-Smirnov tests with Bonferroni-
177 Holme correction were used to compare the 999 maps generated using the
178 randomisation procedure to the maps of observed data.

179

180 High-resolution (0.05 °) mean summer (June 2003 - August 2014) daytime and mean
181 winter (December 2003 – February 2015) night-time land surface temperature data for
182 the study areas were extracted from MODIS data layers (MOD11C3; Land Processes
183 Distributed Active Archive Center 2015) and aggregated to 0.25 ° resolution. UHIs
184 were clearly identifiable in these data (Figs. 1a and 2a). The mean summer and winter
185 temperatures of urban and non-urban cells were compared using separate Mann-
186 Whitney U tests for the UK and Germany. To confidently attribute observed patterns
187 of plant assemblage structure to fine-scale (i.e. UHI) climate variation as opposed to
188 background (i.e. regional) climate variation, a null model representing regional
189 climate without localised UHI warming was used. Mean summer and winter
190 climatology data for a 10-year period (June 1996 – August 2005 and December 1995
191 – February 2005, respectively) were extracted from NCAR's CESM1.0-CAM5
192 climate model (cesm.ucar.edu/models/cesm1.0/cam/) and linearly interpolated to 0.25

193 ° resolution. A zero-censored tobit regression was fitted to combined C₄ relative
194 abundance data for the UK and Germany using only climatology (C₄ relative
195 abundance ~ climatology) and using both climatology and remote-sensed MODIS
196 data (C₄ relative abundance ~ climatology + MODIS). The relative weight of
197 evidence for each of the models was assessed using the Akaike weight, which
198 provides the probability of each model being the best fit for the observed data
199 (Johnson & Omland 2004). A likelihood-ratio test was used to compare the two fitted
200 regressions and test if regional climate alone can explain the observed patterns.

201

202 All analyses were performed in R Statistical Software (R Development Core Team
203 2015) using the *raster* (Hijmans & van Etten 2015) and *ggplot2* (Wickham 2009)
204 packages.

205

206

207 **Results**

208 Urban regions of both the UK and Germany were warmer than non-urban regions
209 (Figs. 1ab and 2ab; Table 1). Summer temperatures of urban regions of the UK were,
210 on average, 3.47 °C warmer than those of non-urban regions (non-urban median
211 temperature = 17.63 °C, urban = 21.10 °C; Mann-Whitney U test: U = 5289, Z = -
212 9.1659, p < 0.0001, r = 0.3699), though winter temperatures were not significantly
213 different (non-urban median temperature = -1.32 °C, urban = -1.23 °C, U = 16687, Z
214 = -9.1659, p = 0.4969, r = 0.0274). Summer temperatures of urban regions of
215 Germany were, on average, 1.98 °C warmer than those of non-urban regions (non-
216 urban median temperature = 22.06 °C, urban = 24.04 °C, U = 8832, Z = -9.9719, p <
217 0.0001, r = 0.3624) and winter temperatures were 1.26 °C warmer in urban regions

218 than in non-urban regions (non-urban median = -5.28 °C, urban = -4.03 °C, U =
219 12288, Z = -8.1136, p < 0.0001, r = 0.2948).
220
221 Plants using the C₄ photosynthetic pathway occurred infrequently in records for both
222 the UK and Germany (median relative abundance of each quarter degree cell: 0.0581
223 % and 0.8372 %, respectively). Urban areas in both countries showed significant
224 increases in C₄ relative abundance compared with non-urban areas (Figs. 1b and 2b).
225 For the UK, the non-urban median C₄ plant proportion was 0.0424 % and the urban
226 proportion was 0.1818 %; a Mann-Whitney U test confirmed the C₄ plant proportions
227 of urban and non-urban cells were significantly different (U = 7200.5, Z = -7.8801, p
228 < 0.0001, r = 0.3180). For Germany the non-urban median C₄ plant proportion was
229 0.7867 % and the urban proportion was 1.2619 %; a Mann-Whitney U test confirmed
230 the C₄ plant proportions of urban and non-urban cells were significantly different (U =
231 11583, Z = -8.4930, p < 0.0001, r = 0.3087). Plant assemblages of large urban areas
232 had particularly high proportions of C₄ plants relative to surrounding non-urban areas
233 (e.g. Greater London, UK, n_{cells} = 7, mean = 0.5742 %, SE = 0.0703 %, adjacent non-
234 urban cells n_{cells} = 9, mean = 0.0161 %, SE = 0.0286 %; Frankfurt/Mainz, Germany,
235 n_{cells} = 14, mean = 1.4225 %, SE = 0.1034 %, adjacent non-urban cells n_{cells} = 20,
236 mean = 0.7615 %, SE = 0.0831 %).
237
238 Species richness contribution of C₄ plants mirrored relative abundance trends with C₄
239 plants contributing a significantly higher proportion of urban richness than non-urban
240 richness. On average, UK C₄ plants accounted for 0.1653 % of species richness in
241 non-urban areas and 0.6515 % of species richness in urban areas (U = 6278.5, Z = -
242 8.5787, p < 0.0001, r = 0.3462). In Germany C₄ plants accounted for a median of

243 1.0874 % of non-urban species richness and 1.6654 % of urban species richness (U =
244 8313, Z = -10.2513, p < 0.0001, r = 0.3726). All patterns of C₄ plant relative
245 abundance and species richness contribution were robust to taxonomic biases and
246 were replicated when angiosperms, monocots, and eudicots were each analysed
247 separately (Table 1, Figs. S1-S4).

248

249 Across urban and non-urban cells of both Germany and the UK, *Amaranthus*
250 *retroflexus* and *Echinochloa crus-galli* were the two most frequently abundant C₄
251 plant species. Neither of these species are native to Europe, the former is a eudicot
252 and the latter is a monocot. The most frequently abundant C₄ species comprised an
253 approximately equal mix of native and non-native species and the majority were
254 monocots (Table S2). In Germany, the five most frequently abundant C₄ species were
255 shared between urban and non-urban cells. Four out of five of these species were
256 grasses, with *A. retroflexus* being the sole exception. Of the five most frequently
257 abundant species in the UK, three were shared between urban and non-urban cells (*A.*
258 *retroflexus*, *E. crus-galli*, and *Cyperus longus*).

259

260 Although cities were generally better sampled than non-urban areas, randomisation
261 procedures could not replicate observed patterns of relative abundance. All
262 randomised maps were significantly different from the observed distributions of C₄
263 plant relative abundance (UK, Kolgorov-Smirnov tests: D mean = 0.4083, p-adjusted
264 mean < 0.0001; Germany, Kolgorov-Smirnov tests: D mean = 0.2545, p-adjusted
265 mean < 0.0001; results of pairwise comparisons between observed data and each
266 random permutation in Tables S3 and S4 respectively).

267

268 Including high-resolution remotely-sensed temperature data, in which UHIs are
269 identifiable, as an independent variable in a zero-censored tobit regression of C₄ plant
270 relative abundance, significantly improved the model fit over a null model using only
271 interpolated climatology data, which represent regional climate but not localised UHI
272 warming, as an independent variable (log-likelihood of null model = 4759.21, log-
273 likelihood of model using high-resolution climate data = 4927.75; likelihood-ratio
274 test: $\chi^2(2) = 337.10, p < 0.0001$; coefficients of each fitted model can be found in
275 Table S5). The magnitude of this improvement was large, with nearly no support for
276 the null model (Akaike weight < 0.0001) and unambiguous support for the model
277 using higher-resolution climate data (Akaike weight > 0.9999; Johnson & Omland
278 2004). Further confidence can therefore be placed in the UHI effect.

279

280

281 **Discussion**

282 In keeping with expectations for temperate climates (Collatz, Berry & Clark 1998;
283 Ehleringer, Cerling & Helliker 1997), C₄ plants had low species richness and relative
284 abundance in plant assemblages across the UK and Germany. Urban areas in both
285 countries did, however, have significantly higher C₄ plant species richness (Figs. S1
286 and S2) and abundance (Figs. 1c and 2c), relative to total plant richness and
287 abundance respectively, than non-urban areas. Nevertheless, species richness
288 contributions of C₄ plants in urban assemblages remained lower than those reported
289 from naturally C₄-dominated assemblages, such as Australian grasses where C₄ plants
290 contribute toward approximately 60 % of total plant richness on average (Hattersley
291 1983). Coastal regions of the UK also show increased proportions of C₄ plants, in
292 agreement with findings from other temperate regions such as Japan, which were

293 attributed to the saline soils and increased irradiance generally found in coastal
294 regions (Hanba, Kobayashi & Enomoto 2009). Furthermore, coastal areas are less
295 likely to experience winter temperatures below freezing (Fig. 1b).

296

297 Patterns of C₃ and C₄ plant distributions and relative abundances, which
298 randomisation procedures confirmed were not an artefact of sampling bias, are
299 primarily driven by temperature variability at a regional scale (Hattersley 1983; Ueno
300 & Takeda 1992; Ehleringer, Cerling & Helliker 1997; Hanba, Kobayashi & Enomoto
301 2009; Pyankov *et al.* 2010; Pau, Edwards & Still 2012; Angelo & Daehler 2015). The
302 background climate variation on which urban areas are overlaid (Zhao *et al.* 2014;
303 Chown & Duffy 2015) cannot, however, explain the observed patterns of high C₄
304 relative abundance in urban plant assemblages. Including high-resolution remotely-
305 sensed temperature data, in which UHIs are identifiable, significantly improves the
306 model fit of a zero-censored tobit regression over a null model that represents regional
307 climate but not localised UHI warming. These patterns must, therefore, be the
308 outcome of fine-scale climatic variation, specifically UHI warming, mediated by the
309 strong physiological link between temperature and comparative photosynthetic yields
310 of C₃ and C₄ plants (Percy & Ehleringer 1984; Sage & Kubien 2007; Yamori,
311 Hikosaka & Way 2013).

312

313 Temperate Europe is perhaps the perfect region in which to identify UHI effects on
314 C₃/C₄ relative abundances. Under mean 2014 CO₂ concentrations of 398.6 ppm
315 (Mauna Loa, Scripps CO₂ Dataset; ~40 Pa under standard atmospheric pressure), 19.5
316 °C has been identified as the crossover temperature at which C₄ grasses gain a
317 competitive advantage over C₃ counterparts (Collatz, Berry & Clark 1998). In

318 temperate Europe, average summer temperatures converge around this threshold
319 temperature, with urban areas significantly warmer than non-urban background
320 temperatures due to UHI warming (Figs. 1a and 2a). C₄ plants are, therefore, more
321 likely to have higher relative fitness in urban areas, where warmer environmental
322 temperatures increase photosynthetic yields (Pearcy & Ehleringer 1984; Sage &
323 Kubien 2007; Yamori, Hikosaka & Way 2013), which may also contribute to gains in
324 C₄ plant biomass (Bijoor *et al.* 2008). Furthermore, freeze-intolerant C₄ plants
325 (Osborne *et al.* 2008) that inhabit urban areas may be insulated from the harshest
326 winter conditions as UHIs homogenise daily and seasonal temperature variations, and
327 decrease the frequency of extreme cold events (Oke 1981; Gaston, Davies &
328 Edmondson 2010; Phelan *et al.* 2015). In turn, C₄ plants are represented by more
329 individuals in urban plant assemblages.

330

331 Examination of species identity indicated that the most frequently abundant C₄ plant
332 species were largely shared across the extent of both countries and repeated across
333 urban and non-urban areas. Patterns of C₄ plant relative abundance therefore appear to
334 be primarily driven by significant increases, relative to the total number of plants, in
335 the urban abundance of a few common C₄ species rather than plants that are unique to
336 urban regions. Nevertheless, the species richness contribution of C₄ plants was also
337 significantly higher in urban regions, which suggests both common and rare species
338 contribute to the observed patterns. Although the majority of C₄ species identified in
339 both urban and non-urban regions were monocots, when monocots are excluded from
340 analyses patterns of C₄ relative abundance remained constant.

341

342 The mechanistic link between C₄ photosynthetic yields and temperature means that
343 UHI warming is the most reasonable explanation for the higher than expected
344 proportion of C₄ plants found in urban areas. Nevertheless, urbanisation results in
345 multiple climatic changes (Seto & Shepherd 2009) that may also influence plant
346 assemblage structure and contribute to trait-based patterns (Williams *et al.* 2015).
347 After temperature, water-availability is thought to be the next-best climatic predictor
348 of C₄ plant distributions (Hattersley 1983; Ehleringer, Cerling & Helliker 1997). The
349 extensive use of low-permeability materials and topographical alterations in urban
350 environments give rise to multiple hydrological changes (Gaston, Davies &
351 Edmondson 2010; e.g. alterations to precipitation, surface-water retention, or
352 humidity). These changes are, however, highly variable amongst cities and show
353 positive, negative and neutral responses relative to the background climate (Seto &
354 Shepherd 2009). Furthermore, despite the association between the evolution of the C₄
355 photosynthesis pathway in plants and arid conditions (Sage, Christin & Edwards
356 2011; Sage 2016), C₄ plants exhibit variable responses to water stress and are no more
357 drought tolerant than C₃ plants under standard conditions (Ghannoum 2009). It is,
358 therefore, unlikely that water-availability, which varies inconsistently amongst cities,
359 is effecting the trait-based patterns described here.

360

361 Physical alterations to the environment brought about by urbanisation processes also
362 have the potential to alter plant assemblage structure (Aronson *et al.* 2014) but, in
363 contrast to UHI warming, these changes are unlikely to affect C₃ and C₄ plants in a
364 consistent manner that explains observed patterns. For example, clearing of trees for
365 construction may have decreased the relative abundance of C₃ plant species in urban
366 cells and altered lightscapes. C₄ photosynthesis is almost completely absent from

367 trees, generally restricted to the herbaceous layer, and C₄ species perform poorly
368 under fluctuating light (Sage 2016). It has, therefore, been suggested that, in addition
369 to the direct removal of C₃ trees, the absence of dense forests and associated
370 understory environments in urbanised areas may benefit C₄ plants (Kubásek, Urban &
371 Šantrůček 2013). Deforestation is not, however, an exclusively urban practice (e.g.
372 agriculture) and described patterns were also apparent when eudicots were excluded
373 from our analyses (Table 1, Figs. S1b and S2b). Furthermore, lightscapes of urban
374 areas are highly variable and studies examining the responses of plants to urbanisation
375 show positive, neutral and negative interactions for both photophilic and photophobic
376 species (Williams, Hahs & Vesk 2015).

377

378 Plant assemblage structure of countries with extended histories of human settlement,
379 such as the UK and Germany, are inevitably shaped by horticultural practices, with
380 species exhibiting certain desirable traits favoured over other species. Which plant
381 traits are desirable, however, is highly subjective and varies substantially based on
382 cultural norms and gardener preferences (Kendal, Williams & Williams 2012).
383 Furthermore, gardens are exclusive to neither urban nor non-urban habitats. Should
384 biases toward certain groups of plants exist between urban and non-urban gardens
385 they likely take the form of taxonomic bias (e.g. favouring grasses) rather than direct
386 selection for or against a plant using a specific photosynthetic pathway. Although it is
387 not possible to completely exclude human preference as a contributing factor to the
388 patterns of C₄ relative abundance described here, separate analysis of eudicot and
389 monocot assemblages (Figs. S1-S4; Table 1) has proven that patterns are robust to
390 higher-level taxonomic bias and cannot, therefore, be due to human preference alone.
391 Habitat affinity has also been identified as a factor that may structure plant

392 assemblages, with plants found in arable fields and settlements characterised by life-
393 history traits that are reflective of the levels of disturbance in their respective
394 environments (Lososová *et al.* 2006). Whether or not this habitat affinity also exists
395 with respect to physiological traits remains untested. Ultimately, the consistency of
396 the spatial signal of the UHI effect across multiple taxa and differing environments in
397 both an island (UK) and continental setting (Germany) suggests that a more
398 fundamental process than habitat affinity of different suites of plants or gardener
399 preference is responsible for the observed patterns.

400

401 Other direct anthropogenic factors must also be considered. Cities are exposed to
402 greater anthropogenic propagule pressure (i.e. propagules introduced directly by
403 human movements) than their non-urban surroundings (Brockerhoff *et al.* 2014). If,
404 therefore, this pressure is biased toward C₄ plant propagules then it may contribute to
405 the observed increases in C₄ plant relative abundance regardless of urban climate
406 effects. A scenario where propagule pressure from C₄ plants is greater than that from
407 C₃ plants is, however, improbable in temperate Europe. Although many C₄ plants are
408 identified as invasive to the region, and invasive species often exhibit common traits
409 (Thompson & McCarthy 2008; van Kleunen, Weber & Fischer 2010; van Kleunen,
410 Dawson & Maurel 2014; though see Leffler *et al.* 2014), the C₄ photosynthetic
411 pathway is not common amongst species that are listed as invasive to either the UK or
412 Germany and the most frequently abundant C₄ plants are a mix of native and non-
413 native species (Table S2). Based on invasive species lists compiled by the DAISIE
414 European Invasive Alien Species Gateway (europe-aliens.org), only 25 of the 671
415 genera that incorporate species invasive in the UK, and 17 of the 413 genera that
416 incorporate species invasive in Germany, contain any species identified as C₄ by

417 either Pyankov *et al.* (2010) or GrassPortal (Osborne *et al.* 2014). Propagule pressure
418 exerted on cities is, therefore, more likely to be biased toward C₃ rather than C₄ plant
419 propagules. The hypothesis that observed patterns are the result of the urban
420 environment being better suited than non-urban environments for the establishment
421 and growth of C₄ plants, be they native or invasive, is more plausible.

422

423 **Future research**

424 Previously, decoupling UHIs, which are one of the most general environmental
425 changes brought about by urbanisation, from other urbanisation impacts has proven
426 difficult. Approaches that combine ecoinformatic and trait-based methods, such as
427 those that have been applied here, are a plausible solution to this problem (Diamond
428 *et al.* 2015; Hahs & Evans 2015; Williams, Hahs & Vesk 2015). They also provide a
429 powerful addition to ecological toolsets, and hold great promise for understanding
430 how environmental variation structures assemblages and communities in response to
431 all forms of anthropogenic change. Indeed, they offer a novel means to give effect to
432 the proposal that urban ecosystems lend themselves to tests of predicted ecological
433 responses to climate change (Youngsteadt *et al.* 2014; Diamond *et al.* 2015).

434

435 In this specific instance, the identification of UHI warming as a significant driving
436 factor of urban patterns of C₄ plant relative abundance provides unique insight into
437 the way in which other plant assemblages might be re-structured with on-going global
438 climate change. Recent observations of increases in the relative abundance of C₄
439 plants in North American grasslands have been attributed to contemporary climatic
440 warming (von Fischer, Tieszen & Schimel 2008) and it is anticipated that broad-scale
441 patterns of C₃ and C₄ plant distribution and abundance will be substantially changed

442 under future climate conditions (Angelo & Daehler 2015). Based on the plant
443 assemblage patterns identified in this study across urban regions, relative abundance
444 of C₄ plants will increase in plant assemblages across temperate Europe as the region
445 warms over the next century. Other ecological responses to UHI warming may also be
446 indicative of the more widespread changes that are to be expected as global
447 temperatures rise. The warming caused by UHIs has already been described altering
448 the phenology of both plants (Zhang *et al.* 2004; Neil & Wu 2006; Gazal *et al.* 2008)
449 and insects (Townroe & Callaghan 2014; Diamond *et al.* 2014) and comparable
450 phenological shifts should be anticipated at global scales under continuing climate
451 change.

452

453 In conclusion, the application of trait-based ecoinformatic methods has provided new
454 insight into the effects of urbanisation on temperate European plant assemblages.
455 Although they remain rare, C₄ plant species represent a significantly larger proportion
456 of plant abundance in urbanised areas than they do in non-urban areas. We have
457 attributed this pattern to warming driven by the urban heat island effect. This
458 hypothesis is supported by physiological differences between C₃ and C₄ plants, which
459 exhibit contrasting responses to environmental warming.

460

461

462 **Acknowledgements**

463 We thank Petr Pyšek, Melodie McGeoch and three anonymous reviewers for their
464 comments on a previous version of the manuscript and all members of the ChownLab
465 for discussion of this work. This work was supported by Australian Research Council
466 Discovery Project DP140101240.

467

468 **Data Accessibility**

469 Occurrence record data are freely available from the GBIF database (www.gbif.org;

470 UK, doi:10.15468/dl.g4lis4; Germany, doi:10.15468/dl.misihs). Data used for all

471 display items and results of randomisation tests are presented in supplementary

472 information.

473

474 **References**

- 475 Angelo, C.L. & Daehler, C.C. (2015) Temperature is the major driver of distribution
476 patterns for C₄ and C₃ BEP grasses along tropical elevation gradients in Hawai‘i,
477 and comparison with worldwide patterns. *Botany*, **93**, 9–22.
- 478 Bijoor, N.S., Czimczik, C.I., Pataki, D.E. & Billings, S.A. (2008) Effects of
479 temperature and fertilization on nitrogen cycling and community composition of
480 an urban lawn. *Global Change Biology*, **14**, 2119–2131.
- 481 Boakes, E.H., McGowan, P.J.K., Fuller, R.A., Chang-Qing, D., Clark, N.E.,
482 O'Connor, K. & Mace, G.M. (2010) Distorted views of biodiversity: spatial and
483 temporal bias in species occurrence data. *PLoS Biology*, **8**, e1000385.
- 484 Brockerhoff, E.G., Kimberley, M., Liebhold, A.M., Haack, R.A. & Cavey, J.F. (2014)
485 Predicting how altering propagule pressure changes establishment rates of
486 biological invaders across species pools. *Ecology*, **95**, 594–601.
- 487 Chown, S.L. & Duffy, G.A. (2015) Thermal physiology and urbanization:
488 perspectives on exit, entry and transformation rules. *Functional Ecology*, **29**,
489 902–912.
- 490 Chown, S.L. & Gaston, K.J. (2016) Macrophysiology - progress and prospects.
491 *Functional Ecology*, **30**, 330–344. doi:10.1111/1365-2435.12510
- 492 Collatz, G.J., Berry, J.A. & Clark, J.S. (1998) Effects of climate and atmospheric CO₂
493 partial pressure on the global distribution of C₄ grasses: present, past, and future.
494 *Oecologia*, **114**, 441–454.
- 495 Collins, R.P. & Jones, M.B. (1985) The influence of climatic factors on the
496 distribution of C₄ species in Europe. *Vegetatio*, **64**, 121–129.
- 497 Diamond, S.E., Cayton, H., Wepprich, T., Jenkins, C.N., Dunn, R.R., Haddad, N.M.
498 & Ries, L. (2014) Unexpected phenological responses of butterflies to the

499 interaction of urbanization and geographic temperature. *Ecology*, **95**, 2613–2621.

500 Diamond, S.E., Dunn, R.R., Frank, S.D. & Haddad, N.M. (2015) Shared and unique
501 responses of insects to the interaction of urbanization and background climate.
502 *Current Opinion in Insect Science*, **11**, 71–77.

503 Duncan, R.P., Clemants, S.E., Corlett, R.T., Hahs, A.K., McCarthy, M.A.,
504 McDonnell, M.J., Schwartz, M.W., Thompson, K., Vesk, P.A. & Williams,
505 N.S.G. (2011) Plant traits and extinction in urban areas: a meta-analysis of 11
506 cities. *Global Ecology and Biogeography*, **20**, 509–519.

507 Ehleringer, J.R., Cerling, T.E. & Helliker, B.R. (1997) C₄ photosynthesis,
508 atmospheric CO₂, and climate. *Oecologia*, **112**, 285–299.

509 Gaston, K.J., Davies, Z.G. & Edmondson, J.L. (2010) Urban environments and
510 ecosystem functions. *Urban Ecology* (ed K.J. Gaston), pp. 35–52. Cambridge
511 University Press, Cambridge.

512 Gazal, R., White, M.A., Gillies, R., Rodemaker, E.L.I., Sparrow, E. & Gordon, L.
513 (2008) GLOBE students, teachers, and scientists demonstrate variable differences
514 between urban and rural leaf phenology. *Global Change Biology*, **14**, 1568–1580.

515 Ghannoum, O. (2009) C₄ photosynthesis and water stress. *Annals of Botany*, **103**,
516 635–644.

517 Hahs, A.K. & Evans, K.L. (2015) Expanding fundamental ecological knowledge by
518 studying urban ecosystems. *Functional Ecology*, **29**, 863–867.

519 Hanba, Y.T., Kobayashi, T. & Enomoto, T. (2009) Variations in the foliar $\delta^{13}\text{C}$ and
520 C₃/C₄ species richness in the Japanese flora of Poaceae among climates and
521 habitat types under human activity. *Ecological Research*, **25**, 213–224.

522 Hattersley, P.W. (1983) The distribution of C₃ and C₄ grasses in Australia in relation
523 to climate. *Oecologia*, **57**, 113–128.

524 Hijmans, R.J. & van Etten, J. (2015) *raster: Geographic analysis and modeling with*
525 *raster data*. <http://CRAN.R-project.org/package=raster>

526 Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution.
527 *Trends in Ecology and Evolution*, **19**, 101-108.

528 Kendal, D., Williams, K.J.H. & Williams, N.S.G. (2012) Plant traits link people's
529 plant preferences to the composition of their gardens. *Landscape and Urban*
530 *Planning*, **105**, 34–42.

531 Kubásek, J., Urban, O. & Šantrůček, J. (2013) C₄ plants use fluctuating light less
532 efficiently than do C₃ plants: a study of growth, photosynthesis and carbon
533 isotope discrimination. *Physiologia plantarum*, **149**, 528–539.

534 Land Processes Distributed Active Archive Center (2015) *MODIS/Terra Land*
535 *Surface Temperature and Emissivity Monthly L3 Global 0.05Deg CMG V6*.
536 *NASA EOSDIS Land Processes DAAC*. USGS Earth Resources Observation and
537 Science (EROS) Center, Sioux Falls, South Dakota (<https://lpdaac.usgs.gov>),
538 10.5067/MODIS/MOD11C3.006.

539 Leffler, A.J., James, J.J., Monaco, T.A. & Sheley, R.L. (2014) A new perspective on
540 trait differences between native and invasive exotic plants. *Ecology*, **95**, 298–305.

541 Lososová, Z., Chytrý, M., Kühn, I., Hájek, O., Horákocá, V., Pyšek, P. & Tichý, L.
542 (2006) Patterns of plant traits in annual vegetation of man-made habitats in
543 central Europe. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 69–
544 81.

545 Michener, W.K. & Jones, M.B. (2012) Ecoinformatics: supporting ecology as a data-
546 intensive science. *Trends in Ecology & Evolution*, **27**, 85–93.

547 Neil, K. & Wu, J. (2006) Effects of urbanization on plant flowering phenology: a
548 review. *Urban Ecosystems*, **9**, 243-257.

549 Oke, T.R. (1981) Canyon geometry and the nocturnal urban heat island: comparison
550 of scale model and field observations. *Journal of Climatology*, **1**, 237–254.

551 Osborne, C.P., Salomaa, A., Kluyver, T.A., Visser, V., Kellogg, E.A., Morrone, O.,
552 Vorontsova, M.S., Clayton, W.D. & Simpson, D.A. (2014) A global database of
553 C₄ photosynthesis in grasses. *The New Phytologist*, **204**, 441–446.

554 Osborne, C.P., Wythe, E.J., Ibrahim, D.G., Gilbert, M.E. & Ripley, B.S. (2008) Low
555 temperature effects on leaf physiology and survivorship in the C₃ and C₄
556 subspecies of *Alloteropsis semialata*. *Journal of Experimental Botany*, **59**, 1743–
557 1754.

558 Pau, S., Edwards, E.J. & Still, C.J. (2012) Improving our understanding of
559 environmental controls on the distribution of C₃ and C₄ grasses. *Global Change*
560 *Biology*, **19**, 184–196.

561 Pearcy, R.W. & Ehleringer, J. (1984) Comparative ecophysiology of C₃ and C₄ plants.
562 *Plant, Cell & Environment*, **7**, 1–13.

563 Peel, M.C. & Finlayson, B.L. (2007) Updated world map of the Köppen-Geiger
564 climate classification. *Hydrology and Earth System Sciences*, **4**, 439–473.

565 Phelan, P.E., Kaloush, K., Miner, M., Golden, J., Phelan, B., Silva III, H. & Taylor,
566 R.A. (2015) Urban heat island: mechanisms, implications, and possible remedies.
567 *Annual Review of Environment and Resources*, **40**, 285–307.

568 Pyankov, V.I., Ziegler, H., Akhiani, H., Deigele, C. & Luetge, U. (2010) European
569 plants with C₄ photosynthesis: geographical and taxonomic distribution and
570 relations to climate parameters. *Botanical journal of the Linnean Society*, **163**,
571 283–304.

572 R Development Core Team. (2015) *A Language and Environment for Statistical*
573 *Computing*. Vienna, Austria.

574 Sage, R.F. (2016) A portrait of the C₄ photosynthetic family on the 50th anniversary
575 of its discovery: species number, evolutionary lineages, and Hall of Fame.
576 *Journal of Experimental Botany*. doi: 10.1093/jxb/erw156

577 Sage, R.F. & Kubien, D.S. (2007) The temperature response of C₃ and C₄
578 photosynthesis. *Plant, Cell & Environment*, **30**, 1086–1106.

579 Sage, R.F., Christin, P.A. & Edwards, E.J. (2011) The C₄ plant lineages of planet
580 Earth. *Journal of Experimental Botany*, **62**, 3155–3169.

581 Schneider, A., Friedl, M.A. & Potere, D. (2010) Mapping global urban areas using
582 MODIS 500-m data: New methods and datasets based on “urban ecoregions.”
583 *Remote Sensing of Environment*, **114**, 1733–1746.

584 Seto, K.C. & Shepherd, J.M. (2009) Global urban land-use trends and climate
585 impacts. *Current Opinion in Environmental Sustainability*, **1**, 89–95.

586 Seto, K.C., Güneralp, B. & Hutyra, L.R. (2012) Global forecasts of urban expansion
587 to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the*
588 *National Academy of Sciences*, **109**, 16083–16088.

589 Thompson, K. & McCarthy, M.A. (2008) Traits of British alien and native urban
590 plants. *Journal of Ecology*, **96**, 853–859.

591 Townroe, S. & Callaghan, A. (2014) British container breeding mosquitoes: the
592 impact of urbanisation and climate change on community composition and
593 phenology. *PLoS One*, **9**, e95325.

594 Ueno, O. & Takeda, T. (1992) Photosynthetic pathways, ecological characteristics,
595 and the geographical distribution of the Cyperaceae in Japan. *Oecologia*, **89**, 195–
596 203.

597 United Nations, Department of Economic and Social Affairs, Population Division
598 (2015). *World Population Prospects: The 2015 Revision, Key Findings and*

599 *Advance Tables*. Working Paper No. ESA/P/WP.241.

600 van Kleunen, M., Dawson, W. & Maurel, N. (2014) Characteristics of successful alien
601 plants. *Molecular Ecology*, **24**, 1954–1968.

602 van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences
603 between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235–245.

604 Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J. & Kattge, J. (2014) The emergence
605 and promise of functional biogeography. *Proceedings of the National Academy of
606 Sciences of the United States of America*, **111**, 13690–13696.

607 von Fischer, J., Tieszen, L. & Schimel, D.S. (2008) Climate controls on C₃ vs. C₄
608 productivity in North American grasslands from carbon isotope composition of
609 soil organic matter. *Global Change Biology*, **14**, 1141–1155.

610 Wickham, H. (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer New
611 York, New York, NY.

612 Williams, N.S.G., Hahs, A.K. & Vesk, P.A. (2015) Urbanisation, plant traits and the
613 composition of urban floras. *Perspectives in Plant Ecology, Evolution and
614 Systematics*, **17**, 78–86.

615 Williams, N.S.G., Schwartz, M.W., Vesk, P.A., McCarthy, M.A., Hahs, A.K.,
616 Clemants, S.E., Corlett, R.T., Duncan, R.P., Norton, B.A., Thompson, K. &
617 McDonnell, M.J. (2009) A conceptual framework for predicting the effects of
618 urban environments on floras. *Journal of Ecology*, **97**, 4–9.

619 Yamori, W., Hikosaka, K. & Way, D.A. (2013) Temperature response of
620 photosynthesis in C₃, C₄, and CAM plants: temperature acclimation and
621 temperature adaptation. *Photosynthesis Research*, **119**, 101–117.

622 Yesson, C., Brewer, P.W., Sutton, T., Caithness, N., Pahwa, J.S., Burgess, M., Gray,
623 W.A., White, R.J., Jones, A.C., Bisby, F.A. & Culham, A. (2007) How global is

624 the global biodiversity information facility? *PLoS ONE*, **2**, e1124.

625 Youngsteadt, E., Dale, A.G., Terando, A.J., Dunn, R.R. & Frank, S.D. (2014) Do
626 cities simulate climate change? A comparison of herbivore response to urban and
627 global warming. *Global Change Biology*, **21**, 97–105.

628 Zhang, X., Friedl, M.A., Schaaf, C.B., Strahler, A.H. & Schneider, A. (2004) The
629 footprint of urban climates on vegetation phenology. *Geophysical Research*
630 *Letters*, **31**, L12209.

631 Zhao, L., Lee, X., Smith, R.B. & Oleson, K. (2014) Strong contributions of local
632 background climate to urban heat islands. *Nature*, **511**, 216–219.

633

634

635 **Table 1:** Results of pairwise Mann-Whitney U tests comparing urban and non-urban
 636 environmental temperature and plant assemblage structure of the UK (urban $n_{\text{cells}} =$
 637 64, non-urban $n_{\text{cells}} = 550$) and Germany (urban $n_{\text{cells}} = 81$, non-urban $n_{\text{cells}} = 676$).
 638

			Urban median	Non-urban median	U	z	p	r	
UK	Temperature (°C)	Day summer	21.1022	17.6337	5289.0	-9.1659	<0.0001	0.3699	
		Night winter	-1.2290	-1.3222	16687.0	-0.6798	0.4969	0.0274	
	C ₄ relative abundance (%)	All plants	0.1818	0.0424	7200.5	-7.8801	<0.0001	0.3180	
		Angiosperms	0.3101	0.0780	8199.5	-7.1231	<0.0001	0.2875	
		Monocots	0.8953	0.0748	7206.0	-8.0698	<0.0001	0.3257	
		Eudicots	0.1293	0.0310	10228.5	-5.6885	<0.0001	0.2296	
	C ₄ richness contribution (%)	All plants	0.6515	0.1653	6278.5	-8.5787	<0.0001	0.3462	
		Angiosperms	0.8588	0.2551	6676.5	-8.2772	<0.0001	0.3340	
		Monocots	2.9873	0.4796	6449.5	-8.6572	<0.0001	0.3494	
		Eudicots	0.3888	0.1336	9060.5	-6.5898	<0.0001	0.2659	
	Germany	Temperature (°C)	Day summer	24.0402	22.0620	8832.0	-9.9722	< 0.0001	0.4024
			Night winter	-4.0250	-5.2833	12288.5	-8.1136	< 0.0001	0.3274
C ₄ relative abundance (%)		All plants	1.2619	0.7867	11583.0	-8.4930	< 0.0001	0.3087	
		Angiosperms	1.3128	0.8192	11428.5	-8.5761	< 0.0001	0.3117	
		Monocots	3.7868	2.4148	9476.0	-9.6260	< 0.0001	0.3499	
		Eudicots	0.6008	0.2906	12427.5	-8.0414	< 0.0001	0.2923	
C ₄ richness contribution (%)		All plants	1.6654	1.0874	8313.0	10.2513	< 0.0001	0.3726	
		Angiosperms	1.7744	1.1391	7839.5	10.5059	< 0.0001	0.3818	
		Monocots	4.6429	3.0303	8454.0	10.1755	< 0.0001	0.3698	
		Eudicots	1.0471	0.5312	10164.5	-9.2586	< 0.0001	0.3365	

639

640

641 **Fig. 1.** Average summer (a) and winter (b) temperature (2000 – 2015) and relative
642 abundance of C₄ plants as a proportion of all plant occurrence records in GBIF (c) for
643 the United Kingdom at 0.25 ° spatial resolution. Cells classified as urban (shaded)
644 were significantly warmer in summer than non-urban cells and had a significantly
645 higher proportion of C₄ plants (Table 1).

646

647 **Fig. 2.** Average summer (a) and winter (b) temperature (2000 – 2015) and relative
648 abundance of C₄ plants as a proportion of all plant occurrence records in GBIF (c) for
649 Germany at 0.25 ° spatial resolution. Cells classified as urban (shaded) were
650 significantly warmer than non-urban cells and had a significantly higher proportion of
651 C₄ plants (Table 1).

652

653 **Table S1:** Results of all analyses for each quarter degree cell. Row names are: xy =
654 coordinates of cell centre, urban_bin = binary classification of urban/non-urban cell,
655 plant_count = count of all plant occurrences for cell, plant_sr = all plants species
656 richness, c4_count = count of all C₄ plants, c4_sr = species richness of all C₄ plants,
657 eudi_count = count of eudicots, eudi_sr = species richness of eudicots, mono_count =
658 count of monocots, mono_sr = species richness of monocots, eudi_c4_count = count
659 of C₄ eudicots, eudi_c4_sr = C₄ eudicot species richness, mono_c4_count = count of
660 C₄ monocots, mono_c4_sr = C₄ monocot species richness, angio_count = count of
661 angiosperms, angio_sr = angiosperm species richness, angio_c4_count = count of C₄
662 angiosperms, angio_c4_sr = C₄ angiosperm species richness, day_summer_temp =
663 MODIS mean daytime summer temperature (2000 – 2015), night_winter_temp =
664 MODIS mean nighttime winter temperature (2000 – 2015), cesm_summer = mean
665 summer temperature from CESM GCM, cesm_winter = mean winter temperature
666 from CESM GCM.

667

668 **Table S2:** Taxonomic data and Native status in Europe for the five most frequently
669 abundant C₄ plant species in urban and non-urban cells of the UK and Germany. †
670 recently reclassified as *Kali* spp., though this is placement is contested
671 (<http://dx.doi.org/10.12705/635.15>).

672

673 **Table S3:** Results of Kolgorov-Smirnov tests for the UK. Pairwise comparisons
674 between observed data and each random permutation.

675

676 **Table S4:** Results of Kolgorov-Smirnov tests for Germany. Pairwise comparisons
677 between observed data and each random permutation.

678

679 **Table S5:** Model fits of zero-censored tobit regressions of C₄ plant relative abundance
680 (%) against a null model using only interpolated climatology data, which represent
681 regional climate but not localised UHI warming, and an Urban heat island (UHI)
682 model incorporating high-resolution remotely-sensed temperature data, in which
683 UHIs are identifiable. Log-likelihood of null model = 4759.21, log-likelihood of UHI
684 model = 4927.75. A likelihood-ratio test confirmed that the UHI model represented a
685 significant improvement in model fit ($\chi^2(2) = 337.10$, $p < 0.0001$).

686

687

688 **Fig. S1.** Relative abundance of C₄ plants as a proportion of angiosperm (a), monocot
689 (b) and eudicot (c) plants based on occurrence records in GBIF for the UK at 0.25 °
690 spatial resolution. Proportions of urban cells (shaded) were significantly different
691 from those of non-urban cells (Table 1).

692

693 **Fig. S2.** Relative abundance of C₄ plants as a proportion of angiosperm (a), monocot
694 (b) and eudicot (c) plants based on occurrence records in GBIF for Germany at 0.25 °
695 spatial resolution. Proportions of urban cells (shaded) were significantly different
696 from those of non-urban cells (Table 1).

697

698 **Fig. S3.** Species richness contribution of C₄ plants as a proportion of richness of all
699 plants (a), monocots (b) and eudicots (c) based on occurrence records in GBIF for the
700 UK at 0.25 ° spatial resolution. C₄ richness contributions for urban cells (shaded)
701 were significantly different from those of non-urban cells (Table 1).

702

703 **Fig. S4.** Species richness contribution of C₄ plants as a proportion of richness of all
704 plants (a), monocots (b) and eudicots (c) based on occurrence records in GBIF for
705 Germany at 0.25 ° spatial resolution. C₄ richness contributions for urban cells
706 (shaded) were significantly different from those of non-urban cells (Table 1).

707

708 **Fig. S5.** C₄ plant relative abundance against mean daytime summer (a) and night-time
709 winter (b) temperatures for the UK. Line represents LOESS smoothed curve with 95
710 % confidence intervals in grey.

711

712 **Fig. S6.** C₄ plant species richness against mean daytime summer (a) and night-time
713 winter (b) temperatures for the UK. Line represents LOESS smoothed curve with 95
714 % confidence intervals in grey.

715

716 **Fig. S7.** C₄ plant relative abundance against mean daytime summer (a) and night-time
717 winter (b) temperatures for Germany. Line represents LOESS smoothed curve with
718 95 % confidence intervals in grey.

719

720 **Fig. S8.** C₄ plant species richness against mean daytime summer (a) and night-time
721 winter (b) temperatures for Germany. Line represents LOESS smoothed curve with
722 95 % confidence intervals in grey.