The phenological response of European vegetation to urbanisation is mediated by macrobioclimatic factors

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Abstract

Plant phenology is a crucial component of ecosystem functioning and is affected by multiple elements of global change; we therefore need to quantify the current phenological changes associated to human activities and understand their impacts on ecosystems. Urbanisation and the intensification of anthropogenic activities alter meteorological conditions and cause phenological changes in urban vegetation worldwide. We used remote sensing data to evaluate the phenological response (start of season date *SOS*, length of season *LOS* and end of season date *EOS*) to urbanisation in the 69 most populated pan-European metropolitan areas (i.e., those that include cities with a population over 450,000 inhabitants) for the period 2002-2021, taking into account the main vegetation types (evergreen forests, deciduous forests, mixed forests, sparse woody vegetation and grasslands). While our findings support previously reported general phenological patterns in response to urbanisation, we found that macrobioclimatic factors strongly determined the strength and direction of the phenological response to urbanisation intensity. In general, SOS advanced and LOS increased with urbanisation intensity across Europe. However, the greatest advances in SOS were registered in metropolitan areas in the Mediterranean region, where there was also more uncertainty in the relationship between SOS and urbanisation. The EOS advanced with urbanisation in metropolitan areas in the Mediterranean macrobioclimate (except for deciduous forests), whereas the opposite trend was observed in metropolitan areas from the Temperate macrobioclimate. Our results suggest that macrobioclimatic constraints operating at the continental scale mediate the relationship between urbanisation intensity and plant phenology.

Keywords. Urbanisation; plant phenology; remote sensing; Europe; macrobioclimates; vegetation types.

Introduction

Plant phenology is a crucial component of ecosystem functioning because of its role in the carbon cycle (Piao et al., 2023), feedbacks on local and regional climate (Richardson et al., 2013) and the assembly of ecological communities (Inouye, 2022; Renner & Zohner, 2018). It also has important repercussions from the point of view of public-health as is the case of the flowering phenology of species with high allergenic potential (Bernard-Verdier et al., 2022; Rojo et al., 2021).

Plant phenology is sensitive to nutrient and water availability and changes in temperature and photoperiod (Piao et al., 2023); accordingly, over the last decades scientists have been making great efforts to quantify phenological changes in response to the multiple components of global change and to understand their consequences on ecosystems (Garcia et al., 2014; Menzel et al., 2020). The intensification of urbanisation and anthropogenic activities alter meteorological conditions at the local scale and affect the dynamics of urban vegetation (Trusilova & Churkina, 2008). Higher air and land surface temperatures in cities compared to the surrounding rural areas – a phenomenon referred to as the urban heat island – is the most prominent driver of phenological changes associated to urbanisation (Jochner & Menzel, 2015; Meng et al., 2020; Neil & Wu, 2006). Plants' phenological response is also affected by other meteorological changes derived from urbanisation such as a decrease in air humidity (Hao et al., 2018), and stressors such as limited space for growth, soil compaction and pollution (Czaja et al., 2020).

Data gathered from ground stations and satellite observations have made it possible to unveil the general responses of plant phenology to urbanisation. Most studies agree that spring phenophases (i.e., flowering, leaf-out and bud opening) tend to start earlier in response to the urban heat island associated to the intensification of urbanisation across world regions (Jia et al., 2021; Li et al., 2019; Meng et al., 2020; Ren et al., 2018; Wohlfahrt et al., 2019; Yang et al., 2020). The opposite trend – i.e., delay in spring phenophases with urbanisation – has occasionally been reported for specific plant functional types (Galán Díaz et al., 2023; Y. Zhang

et al., 2022), which may indicate that some plant species do not adequately meet their chilling requirements due to rising autumn and winter temperatures (Inouye, 2022; Piao et al., 2023; Yu et al., 2010). Most studies also report delays in autumn phenophases (e.g., leaf senescence) caused by urbanisation (Ren et al., 2018; Wohlfahrt et al., 2019; Yang et al., 2020). However, less consistent trends have been found between urbanisation intensity and autumn phenophases, probably because they strongly depend on other factors such as photoperiod, preseason forcing and productivity rates during the growth season (Keenan & Richardson, 2015; Wu et al., 2018; Zani et al., 2020).

The direction and strength of these general patterns are affected by other factors such as plant functional type and regional climate. The response of different vegetation types to urbanisation is mediated on the one hand by temperature sensitivity and physiological constraints. For instance, annual plants, early-flowering species and lower-growing perennials with a higher specific leaf area show the greatest advances in their spring phenophases (Inouye, 2022; Li et al., 2019; Neil & Wu, 2006). Contrasting phenological responses to urbanisation have previously been found between deciduous and evergreen species; hence leaf longevity also plays an important role (Galán Díaz et al., 2023; Y. Zhang et al., 2022). On the other hand, regional climate affects the daily and seasonal relationship between urbanisation intensity and land surface temperatures (Sismanidis et al., 2022; Wienert & Kuttler, 2005). For instance, in mainland China, Ma et al. (2016) reported a stronger relationship between urbanisation and summer land surface temperature in dry and cold regions compared to wet and hot regions. We might therefore expect plants' phenological response to urbanisation to depend on regional climate.

Recent efforts to understand the effect of urbanisation on plant phenology in Europe using ground observations have reported that flowering, fruiting and leaf-out dates occurred an average of 1.0-4.3 days earlier in completely urbanised compared to non-urbanised areas (Li et al., 2019; Wohlfahrt et al., 2019); and that leaf senescence tended to occur 1.3–2.7 days later (Wohlfahrt et al., 2019). Although these studies provide invaluable information on the response

of several phenophases of individual species to urbanisation, they mostly focused on Europe's Temperate region, where most of the observations were carried out (Templ et al., 2018). We argue that the use of other data sources and methodologies will offer new insights into the relationship between urbanisation and plant phenology in Europe, especially in the little studied plant phenological response to urbanisation in Mediterranean Europe.

In this study we used remotely sensed data to quantify the impact of urbanisation intensity on the phenology of evergreen, deciduous and mixed forests, sparse woody vegetation (i.e., forest canopy cover of less than 60%) and grasslands in the main 69 pan-European metropolitan areas (i.e., those that include cities with a population over 450,000 inhabitants) for the period 2002-2021. We hypothesised that: (i) urbanisation brings forward the start of the season (SOS) of European vegetation, increases its length (LOS) and delays its end (EOS); (ii) the main vegetation types respond differently to urbanisation; and (iii) the phenological response of vegetation to urbanisation depends on regional temperature and varies between the two main macrobioclimates present in Europe (Temperate vs. Mediterranean).

Material and methods

Study area

The study area comprises the main 69 pan-European metropolitan areas (Figure 1). Taking advantage of the fact that urbanisation data was also available for Turkey, we considered cities from the Mediterranean areas of this country in order to have a greater representation of cases from the Mediterranean macrobioclimate. The study area comprises two macrobioclimatic regions, i.e., Temperate and Mediterranean. In contrast to the Temperate, the Mediterranean macrobioclimate is characterised by having at least two consecutive dry months during the hottest period of the year (Rivas-Martínez et al., 2002). For each European city with a population over 450,000, we set a surrounding buffer that was two times the area of its urban extent using Zhao et al.'s (2022) global dataset of annual urban extents from night-time lights. This ensured an equal representation of urban, peri-urban and rural areas. Cities located within

each other's buffer area were treated as the same metropolitan area. For instance, Amsterdam, Rotterdam, The Hague and surrounding cities were merged within the metropolitan area of Randstad; and Köln, Essen, Dortmund, Düsseldorf, Duisburg and nearby cities were merged within the Rhine-Ruhr metropolitan area.

Data collection

Phenology and land-use data were obtained from MODIS and downloaded using MODISTools (Hufkens, 2022). Start of season (SOS) and end of season (EOS) dates correspond to the Greenup and Dormancy layers of the Land Cover Dynamics Yearly L3 Global 500 m dataset (MCD12Q2 v006) derived from the Enhanced Vegetation Index 2. SOS and EOS respectively are the day of the year (doy) when the vegetation index first and last crossed 15% of the segment of its amplitude. Length of season (LOS) is the number of days between the SOS and EOS. Land cover data was obtained from the LC_Type1 layer of the Land Cover Type Yearly L3 Global 500 m dataset (MCD12Q1 v006) and corresponds to the Annual International Geosphere-Biosphere Programme (IGBP) classification system. We aggregated the land uses of the IGBP classification into five main vegetation types: evergreen forests (classes 1 and 2), deciduous forests (classes 3 and 4), mixed forests (class 5), sparse woody vegetation (i.e., forest canopy cover less than 60%) (classes 8 and 9) and grasslands (class 10).

We used two datasets from the Copernicus Land Monitoring Service at a 100 m resolution to estimate urbanisation intensity: (i) CORINE Land Cover and (ii) Imperviousness Density. The CORINE Land Cover Inventory was available for the years 2000, 2006, 2012 and 2018. We considered urbanised areas to be those in the categories of continuous urban fabric, discontinuous urban fabric, industrial or commercial units, road and rail networks and associated land, port areas and airports. The Imperviousness Density dataset indicates the percentage of soil sealing and was available for the years 2006, 2009, 2012, 2015 and 2018. Both datasets were linearly interpolated to cover the entire period of 2002-2021 using the *approximate* function implemented in the *terra* R package (Hijmans et al., 2022). For each phenological observation (i.e., centroid of each 500m^2 pixel from MODIS), urbanisation

intensity was computed as the proportion of urbanised area (i.e., CORINE dataset) and average soil sealing (i.e., Imperviousness Density) within a circular buffer with a 250m, 500m and 1km radius.

Land surface temperature (LST) was obtained from the MODIS Land Surface Temperature/Emissivity 8-Day L3 Global 1 km dataset (MOD11A2 v006) and downloaded using the *MODISTools* R package (Hufkens, 2022). Elevation and global climate data were obtained from Worldclim v2.1 at a resolution of 30 seconds (Fick & Hijmans, 2017).

Data analysis

First, we determined the effect that the source of urbanisation intensity and buffer choice had on the analyses. For each metropolitan area, we ran six multiple regression models using SOS as the response variable, and each combination of urbanisation source (i.e., CORINE Land Cover and Imperviousness Density) and buffer size (250m, 500m and 1km radius) as the explanatory variable, including elevation and year as covariables. We then computed the Pearson coefficient among the regression coefficients of urbanisation (β_U^{SOS}) obtained from the different models. There was a high linear correlation among the phenological responses of SOS to the different proxies of urbanisation intensity (Appendix A). We used CORINE Land Cover at 500 m for subsequent analyses, which is also supported by a previous study (Wohlfahrt et al., 2019).

Second, for each metropolitan area, we used two statistical approaches to analyse the phenological response of the five main vegetation types to urbanisation. (i) We implemented a random forest model using the *randomForest* R package (Liaw & Wiener, 2002) and used partial dependent plots provided by the *pdp* R package (Greenwell, Brandon, 2017) to explore the general patterns. (ii) We performed multiple linear regressions to quantify the effect (i.e., regression coefficients). We used the phenological indexes (SOS, LOS and EOS) as the response variables and urbanisation and year as explanatory variables, also including elevation as a covariable to control for this crucial factor (Ziello et al., 2009).

Third, we explored whether the phenological response to urbanisation in European metropolitan areas depended on regional climate. This was done by first studying whether the phenological response to urbanisation (i.e., β_U^P) depends on annual mean temperature. We used annual mean temperature because it is closely correlated to other climate variables at the continental scale, and is known to influence the urban heat island (Ma et al., 2016; Wienert & Kuttler, 2005) and the phenological response of plants to urbanisation (Li et al., 2019). We also performed simple linear regressions with the 19 BIOCLIM variables (Booth et al., 2014) available from WorldClim to explore potential drivers. We then compared the phenological response of vegetation types to urbanisation in the metropolitan areas in Europe's two main macrobioclimates: Temperate vs. Mediterranean (Rivas-Martínez et al., 2002). The classification of macrobioclimates relates to the earth's main climates, biomes and biogeographical regions and provides a simple interpretation and delimitation of the main bioregions of Europe.

Fourth, we explored whether the relationship between LST and urbanisation (β_U^{LST}) and year (β_Y^{LST}) varies between metropolitan areas in the Mediterranean and Temperate macrobioclimates and depends on regional temperature. For this, we ran multiple linear regressions using urbanisation intensity, year and elevation as explanatory variables.

All analyses were performed in R (version 4.2.2). The codes used in this study are available at GitHub (https://github.com/galanzse/europe_urbantrees).

Results

The random forest model showed that, as the intensity of urbanisation rose, the start of season date (SOS) advanced and the length of season (LOS) increased in all the main vegetation types (Figure 2). Specifically, we found a significant advance in SOS with urbanisation intensity in 59.02% of cases (vegetation type × metropolitan area) when data was available, and a significant delay in 10.66% of cases (Table 1; Figure 3). Increasing urbanisation intensity resulted in a significant lengthening of the LOS in 57.38% of cases, and a shortening in 8.61%.

The relationship between the end of season date (EOS) and urbanisation intensity resulted significantly positive in 41.80% of cases (i.e., delay of EOS) and significantly negative in 20.08% (i.e., advance in EOS) (Table 1; Figure 3). We found contrasting responses of EOS to urbanisation among vegetation types. The EOS of deciduous forests advanced on average 0.03 days per 1% increase in urbanisation intensity, whereas the EOS of evergreen forests, mixed forests and grasslands was delayed by 0.01-0.17 days per unit increase in urbanisation intensity. The regression coefficients per metropolitan areas and vegetation type can be found in Appendix B.

Our results also revealed significant phenological shifts along the time series (Table 1, Figure 3). The SOS of deciduous and evergreen forests, grasslands and sparse woody vegetation has advanced at a rate of 0.02-0.40 days/year over the last two decades. The LOS of deciduous, evergreen and mixed forests and sparse woody vegetation has increased by 0.15-0.30 days/year over the last two decades. On average, the EOS of deciduous and mixed forests has been delayed by 0.13-0.14 days/year since 2002.

Annual mean temperature was a good explanatory variable of the strength of the response of SOS and EOS to urbanisation intensity in European metropolitan areas (Table 2; Figure 4). Isothermality and precipitation of the wettest quarter were also significant but are spatially correlated to annual mean temperature at a continental scale. The advance of the SOS with increasing urbanisation was significantly most intense as annual mean temperature increased, whereas it tended to zero in colder metropolitan areas. LOS was not significantly affected by regional temperature. We found a significant relationship between the effect of urbanisation on the EOS and annual mean temperature: urbanisation tended to delay the EOS of vegetation in metropolitan areas with annual mean temperatures below 11ºC (i.e., metropolitan areas in the Temperate macrobioclimate), whereas it mostly brought forward the EOS of vegetation in metropolitan areas with annual mean temperatures over 11ºC (i.e., metropolitan areas in the Mediterranean macrobioclimate). The uncertainty in the relationship between the phenological indexes and urbanisation intensity also increased with annual mean temperature (Figure 4), i.e.,

in metropolitan areas in the hottest regions there was a greater average phenological response to urbanisation intensity compared to colder areas, but also more variability associated to the model.

The phenological response of the different vegetation types to urbanisation (β_U^P) depended on the regional macrobioclimate (Table 3; Figure 5; results of random forest are available in Appendix C). In metropolitan areas in the Temperate macrobioclimate, we found consistent advances in the SOS, increased LOS and delays in the EOS across vegetation types with increasing urbanisation intensity (except for an advance in the EOS of deciduous forests). Vegetation in metropolitan areas in the Mediterranean macrobioclimate showed less consistent responses to urbanisation.

LST increased with urbanisation across European metropolitan areas (Figure 6a). The rate of increase in LST with urbanisation (β_U^{LST}) decreased with annual mean temperature, and was greater in Temperate than in Mediterranean metropolitan areas during both day and night. β_U^{LST} in Temperate metropolitan areas was greater during spring (MAM) and summer (JJA). LST has increased over the last two decades across European metropolitan areas (Figure 6b). Metropolitan areas in the Temperate macrobioclimate showed an especially sharp rise in winter temperatures (DJF).

Discussion

General response of vegetation phenology to urbanisation

We have found strong evidence that urbanisation advances the SOS and increases the LOS of deciduous, evergreen and mixed forests, sparse woody vegetation and grasslands across metropolitan areas of Europe. Our results using remotely sensed phenological data support those of Li et al. (2019) and Wohlfahrt et al. (2019) who, using species-level data from the Pan European Phenology Database (PEP725), found that leaf-out occurred 1.0-4.3 days earlier in completely urbanised compared to non-urbanised areas. We provide higher estimates of phenological changes associated to urbanisation compared to these studies: we report that the

SOS of vegetation in completely urbanised areas occurred 3-19 days earlier compared to the surrounding natural vegetation. It has been demonstrated that highly heterogeneous pixels interfere in the phenological signal (Alonzo et al., 2023) and that the SOS detected is biased towards earlier SOS dates because of the higher diversity of spring phenology dates per pixel in urban areas (Tian et al., 2020; X. Zhang et al., 2017). Our results are therefore probably overestimated due to the use of phenological data at a coarse resolution (i.e., 500 m). Observation conditions increase the uncertainty in the phenological data detected using remote sensing instruments compared to ground-based observations, and the choice of vegetation indexes, curve-fitting methods and thresholds to calculate the different phenophases makes it difficult to compare studies (Zeng et al., 2020). However, beyond the discrepancies in the intensity of the phenological response, the general pattern for the SOS and LOS is quite consistent with those reported across regions by most of the previous literature (Meng et al., 2020; Pan et al., 2021; Yang et al., 2020). Our results show the general continuous pattern of the phenological change along the complete urbanisation gradient which is not always provided.

The end of season date (EOS) was frequently delayed (around 1 to 13 days) in completely urbanised areas. Wohlfahrt et al. (2019) found that leaf senescence occurred 1.3–2.7 days later in completely urbanised compared to non-urbanised areas in Europe. However, we provide evidence that the influence of urbanisation on EOS is less consistent compared to the other phenological indexes as it depends on the vegetation type and regional temperature. The relationship between EOS and urbanisation for deciduous forests was most frequently negative. On the one hand, it has been observed that the dates of leaf senescence have advanced in broadleaf trees from Central Europe and North America (Keenan & Richardson, 2015; Zani et al., 2020). The correlation between the dates of spring budburst and leaf senescence might show that earlier spring phenophases counteract the influence of warmer autumn temperatures via structural and physiological constraints on leaf longevity, or an increase probability of frost damage to buds and leaves (Keenan & Richardson, 2015). Earlier leaf-out has been demonstrated to lead to an advance in plants' seasonal cycles via increased photosynthetic

activity, causing earlier carbon saturation and inducing leaf senescence (Zani et al., 2020). On the other hand, the category "deciduous forests" in our dataset occurred mostly in areas where urbanisation intensity did not exceed 50%; we might therefore expect urbanisation to elicit a weaker phenological response compared to the other vegetation types.

Contrasting results have been reported in the literature regarding the relationship between autumn phenophases and urbanisation (reviewed in Jochner & Menzel, 2015), reflecting the importance of other factors such as photoperiod (Wu et al., 2018). The contrasting response of EOS to urbanisation was not only observed between vegetation types; as discussed below, vegetation from the Mediterranean and Temperate macrobioclimates showed different behaviours in this phenological index which underlines the remarkable influence of macrobioclimatic factors.

Our results showed contrasting sensitivities of vegetation types and life forms to the meteorological changes derived from urbanisation that influence spring and autumn phenophases (Li et al., 2019). These differences observed among plant functional types makes it strongly inadvisable to group observations by wider ecosystem types as is frequently the case in urban phenological studies (e.g., Jia et al., 2021; Yang et al., 2020; Y. Zhang et al., 2022). Some of our findings require further enquiry and the use of *in situ* observations to reduce the uncertainties associated to mapping land uses at a coarse scale, e.g., the delay SOS of Mediterranean evergreen forests with urbanisation in certain metropolitan areas (Galán Díaz et al., 2023) or the wide variation in the phenological response of Mediterranean evergreen forests and grasslands to urbanisation across metropolitan areas.

Spatial differences in the phenological response to urbanisation: effect of macrobioclimate

Regional mean annual temperature affected the strength, direction and uncertainty of the response of the SOS and EOS to urbanisation in European vegetation. Using population density as a proxy for urbanisation, Li et al. (2019) found a negative relationship between SOS and urbanisation across cold areas of Europe and North America. Our results suggest that the SOS

of deciduous, evergreen and mixed forests, sparse woody vegetation and grasslands in Europe advances with increasing urbanisation, although the strength and uncertainty of this relationship increased with annual mean temperature. The most marked phenological advances were registered in metropolitan areas from the Mediterranean region, but this is also where there was more uncertainty in the relationship between SOS and urbanisation, which could be explained by physiological stress caused by increasing preseason and spring temperatures (Fu et al., 2015). Our results also indicate that the effect of urbanisation intensity on land surface temperature (related to the urban heat island) is stronger in metropolitan areas in the Temperate macrobioclimate throughout the day and the year, as noted in previous studies (Ma et al., 2016; Wienert & Kuttler, 2005). In Europe, we can therefore expect a more consistent phenological response to urbanisation in metropolitan areas in northern latitudes, whereas in southern cities in the Mediterranean macrobioclimate the uncertainty observed could be explained by the interplay of other factors such as water availability or proximity to the coast, which may play an important role (Richardson et al., 2013; Yang et al., 2020).

The EOS of all vegetation types was positively correlated with urbanisation intensity in metropolitan areas with annual mean temperatures below 11ºC (most metropolitan areas in the Temperate macroclimate), except for deciduous forest as indicated above. In metropolitan areas with annual mean temperatures over 11ºC (most metropolitan areas in the Mediterranean macroclimate), the response was more heterogeneous but mostly negative, i.e., the EOS advanced in highly urbanised areas. Increasing summer and autumn temperatures as a result of urbanisation might reduce water availability in the dry regions of the Northern Hemisphere, where water already constitutes a limiting factor, subsequently increasing plant stress, limiting plant growth and advancing the EOS (Liu et al., 2016). Garonna et al. (2014) also found that, as opposed to vegetation in northern Europe, the EOS of vegetation in the Mediterranean region of Europe advanced around 7.5 days during the period 1982-2011, also showing great spatial heterogeneity. We observed that day and night temperatures have increased throughout the year in recent decades. In this context, we can expect physiological stress induced by higher

temperatures and summer drought to be a major limiting factor for plant growth at the end of the season in vegetation in the Mediterranean macrobioclimate (Menzel et al., 2020; Richardson et al., 2013). Our results suggest that macrobioclimatic constraints operating at the continental scale play an important role in determining the direction of the effect of urbanisation intensity on autumn phenophases.

Phenological changes for the period 2002-2021

After removing the urbanisation effect, our results showed that the average SOS of the vegetation types advanced 4.68 ± 2.83 days (mean ± sd) and the LOS was extended 3.8 ± 2.33 days in the last two decades. Although the aim of our paper was not to quantify temporal changes on phenology in European vegetation, these results, coupled with the uncertainty in the temporal changes in EOS, have been widely reported in Europe (Gordo & Sanz, 2009; Menzel et al., 2020; Vogel, 2022). Furthermore, quantifying changes in the response of plant phenology to urbanisation in a context of global warming is challenging because we can expect the urban heat island effect to decrease as temperature increases (Ma et al., 2016).

Conclusions

We have quantified the impact of urbanisation on the most populated European metropolitan areas. This contribution is among the first evidence to explore the macrobioclimatic factors that drive the spatial variability observed in the phenological response to urbanisation considering the entire Mediterranean-Temperate gradient and using remote sensing data at the continental scale. Our results highlight the importance of considering vegetation functional types and large climatic gradients to fully comprehend the impact of urbanisation on urban vegetation. It is worth noting that both the strength and direction of the effect of urbanisation on plant phenology varied at the continental scale, and showed greater uncertainty in metropolitan areas in the Mediterranean macrobioclimate.

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Author's contributions. JGD: Conceptualisation, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review and editing. AMGB: Investigation, Writing - review and editing. JR: Conceptualisation, Methodology, Formal analysis, Investigation, Writing - review and editing.

Competing interests. The authors have declared that no competing interests exist.

Data availability. This work was developed using open source datasets. The codes used in this study are available at GitHub (https://github.com/galanzse/europe_urbantrees).

Tables

Table 1. Phenological response (mean and standard deviation) of the five vegetation types to urbanisation (β_U^P) and time (β_Y^P) calculated using a multiple regression model including elevation as a covariable. We explored if the distribution of regression coefficients was significantly different from zero by running t-tests. SOS: start of season date, LOS: length of season in days, EOS: end of season date.

		β_U^P				β_Y^P			
pheno	**vegetation**	**mean ± sd**	**t**	**df**	**p**	**mean ± sd**	**t**	**df**	**p**
SOS (doy)	evergreen forests	0.02 ± 0.49	0.18	18	0.859	-0.28 ± 0.52	-2.05	13	0.061
	grasslands	-0.05 ± 0.18	-1.89	45	0.065	-0.4 ± 0.97	-3.12	56	0.002
	mixed forests	-0.19 ± 0.23	-4.36	28	0.000	-0.02 ± 0.33	-0.33	24	0.740
	sparse woody vegetation	-0.11 ± 0.14	-6.38	63	0.000	-0.25 ± 0.69	-2.76	55	0.007
	deciduous forests	-0.16 ± 0.12	-4.53	11	0.001	-0.19 ± 0.2	-3.75	16	0.001
LOS (days)	evergreen forests	0.15 ± 0.42	1.18	10	0.264	0.25 ± 0.71	1.30	13	0.214
	grasslands	0.09 ± 0.2	3.39	56	0.001	0.15 ± 1.1	1.03	56	0.308
	mixed forests	0.16 ± 0.27	3.47	30	0.002	0.18 ± 0.32	3.21	30	0.003
	sparse woody vegetation	0.11 ± 0.11	7.27	49	0.000	0.29 ± 0.61	3.64	57	0.000
	deciduous forests	0.1 ± 0.14	2.55	11	0.027	0.3 ± 0.19	6.30	15	0.000
EOS (doy)	evergreen forests	0.17 ± 0.64	1.03	13	0.322	-0.04 ± 0.47	-0.31	11	0.764
	grasslands	0.05 ± 0.26	1.42	53	0.162	-0.28 ± 1.21	-1.75	54	0.085
	mixed forests	0 ± 0.12	0.15	13	0.881	0.13 ± 0.16	4.27	27	0.000
	sparse woody vegetation	-0.02 ± 0.16	-1.14	56	0.260	0.05 ± 0.91	0.42	54	0.673
	deciduous forests	-0.03 ± 0.1	-0.96	11	0.357	0.14 ± 0.19	2.51	11	0.028

Table 2. Results of simple linear regressions using the phenological indexes as the response variable and each of the 19 BIOCLIM variables available from WorldClim as explanatory variables. SOS: start of season date, LOS: length of season in days, EOS: end of season date. BIO1: annual mean temperature, BIO2: mean diurnal range, BIO3: isothermality, BIO4: temperature seasonality, BIO5: max temperature of warmest month, BIO6: min temperature of coldest month, BIO7: temperature annual range, BIO8: mean temperature of wettest quarter, BIO9: mean temperature of driest quarter, BIO10: mean temperature of warmest quarter, BIO11: mean temperature of coldest quarter, BIO12: annual precipitation, BIO13: precipitation of wettest month, BIO14: precipitation of driest month, BIO15: precipitation seasonality, BIO16: precipitation of wettest quarter, BIO17: precipitation of driest quarter, BIO18: precipitation of warmest quarter, BIO19: precipitation of coldest quarter.

	SOS (doy)			LOS (days)			EOS (doy)		
BIOCLIM	**β**	**R^2**	**p**	**β**	**R^2**	**p**	**β**	**R^2**	**p**
bio1	-0.015	0.07	0.000				-0.027	0.16	0.000
bio2	-0.011	0.03	0.015	-0.010	0.02	0.045	-0.024	0.11	0.000
bio3	-0.014	0.10	0.000				-0.022	0.16	0.000
bio4	0.000	0.05	0.002	0.000	0.03	0.017			
bio5	-0.002	0.08	0.000						
bio6				0.003	0.04	0.005	0.003	0.03	0.018
bio7				-0.003	0.05	0.003	-0.003	0.06	0.002
bio8	-0.001	0.07	0.001						
bio9				0.001	0.06	0.002	0.001	0.03	0.018
bio10				0.001	0.04	0.004	0.001	0.08	0.000
bio11	-0.001	0.04	0.008				-0.001	0.04	0.006
bio13							-0.014	0.07	0.001
bio14	0.000	0.07	0.000				0.000	0.04	0.011
bio15				-0.009	0.02	0.047	-0.018	0.08	0.000
bio16	-0.016	0.11	0.000				-0.022	0.15	0.000
bio17	0.012	0.05	0.002						
bio19				-0.004	0.02	0.031	-0.007	0.09	0.000

Table 3. Phenological response (mean and standard deviation) to urbanisation and time of the main vegetation types in Mediterranean and Temperate metropolitan areas expressed as the regression coefficients (β_U^P and β_Y^P) obtained from multiple regression models using elevation as a covariable. We explored whether the distribution of regression coefficients was significantly different from zero by running t-tests. There was only one observation of deciduous and mixed forests in metropolitan areas from the Mediterranean macrobioclimate. SOS: start of season date, LOS: length of season in days, EOS: end of season date.

		β_U^P Mediteranean				β_U^P Temperate			
pheno	**vegetation**	**mean ± sd**	**t**	**df**	**p**	**mean ± sd**	**t**	**df**	**p**
SOS (doy)	evergreen forests	0.38 ± 0.89	0.97	4	0.385	-0.11 ± 0.13	-3.05	13	0.009
	grasslands	-0.04 ± 0.29	-0.67	15	0.509	-0.05 ± 0.09	-3.13	29	0.004
	mixed forests	-0.57 ± 0.58	-1.71	2	0.228	-0.14 ± 0.12	-5.94	25	0.000
	sparse woody vegetation	-0.21 ± 0.24	-3.63	17	0.002	-0.08 ± 0.05	-9.43	45	0.000
	deciduous forests	-0.25 ± 0.03	-10.50	1	0.060	-0.14 ± 0.13	-3.54	9	0.006
LOS (days)	evergreen forests	-0.14 ± 0.92	-0.22	1	0.858	0.21 ± 0.3	2.16	8	0.062
	grasslands	-0.01 ± 0.27	-0.15	16	0.877	0.13 ± 0.14	5.78	39	0.000
	mixed forests	0.38 ± 0.64	1.33	4	0.254	0.12 ± 0.1	6.43	25	0.000
	sparse woody vegetation	0.06 ± 0.2	0.92	7	0.386	0.12 ± 0.08	9.40	41	0.000
	deciduous forests	0.19 ± 0.01	14.68	1	0.043	0.09 ± 0.15	1.84	9	0.098
EOS (doy)	evergreen forests	0.26 ± 1	0.65	5	0.543	0.1 ± 0.19	1.59	7	0.154
	grasslands	-0.04 ± 0.42	-0.44	14	0.661	0.09 ± 0.16	3.48	38	0.001
	mixed forests	0.19				0 ± 0.12	-0.25	12	0.801
	sparse woody vegetation	-0.19 ± 0.2	-3.73	14	0.002	0.03 ± 0.08	2.85	41	0.007
	deciduous forests	-0.09				-0.02 ± 0.11	-0.72	10	0.488

Figures

Figure 1. Metropolitan areas included in this study and annual mean temperature for the period 1970-2000. Metropolitan areas were classified according to their macrobioclimate in Mediterranean (red) and Temperate (blue) according to Rivas-Martínez et al. (2002).

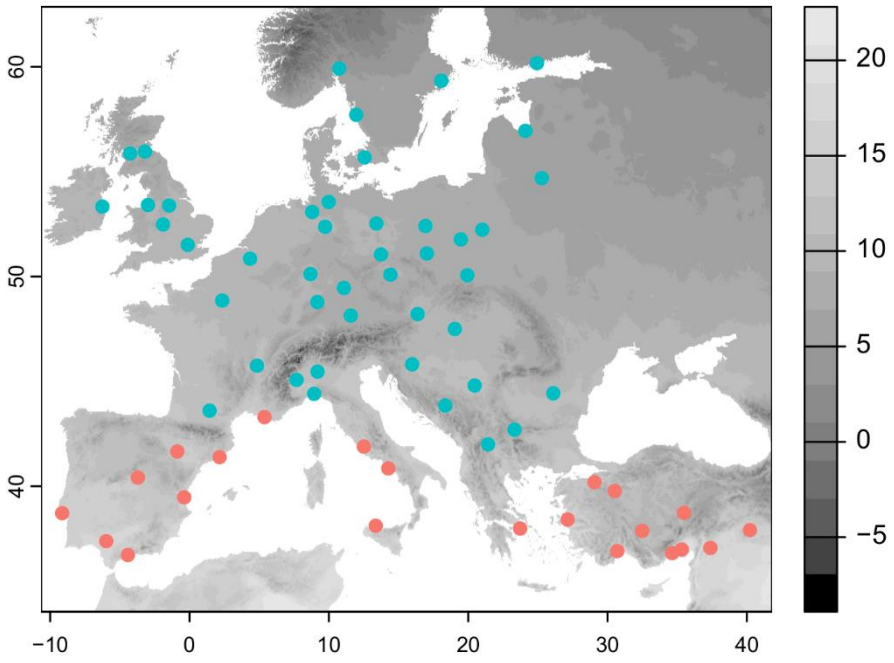


Figure 2. Partial effect of urbanisation intensity on the phenological indexes. Random forest models for each metropolitan area were performed to predict the general phenological response to urbanisation. The phenological variable for each metropolitan area was normalised by subtracting the mean and dividing by the standard deviation. SOS: start of season date, LOS: length of season in days.

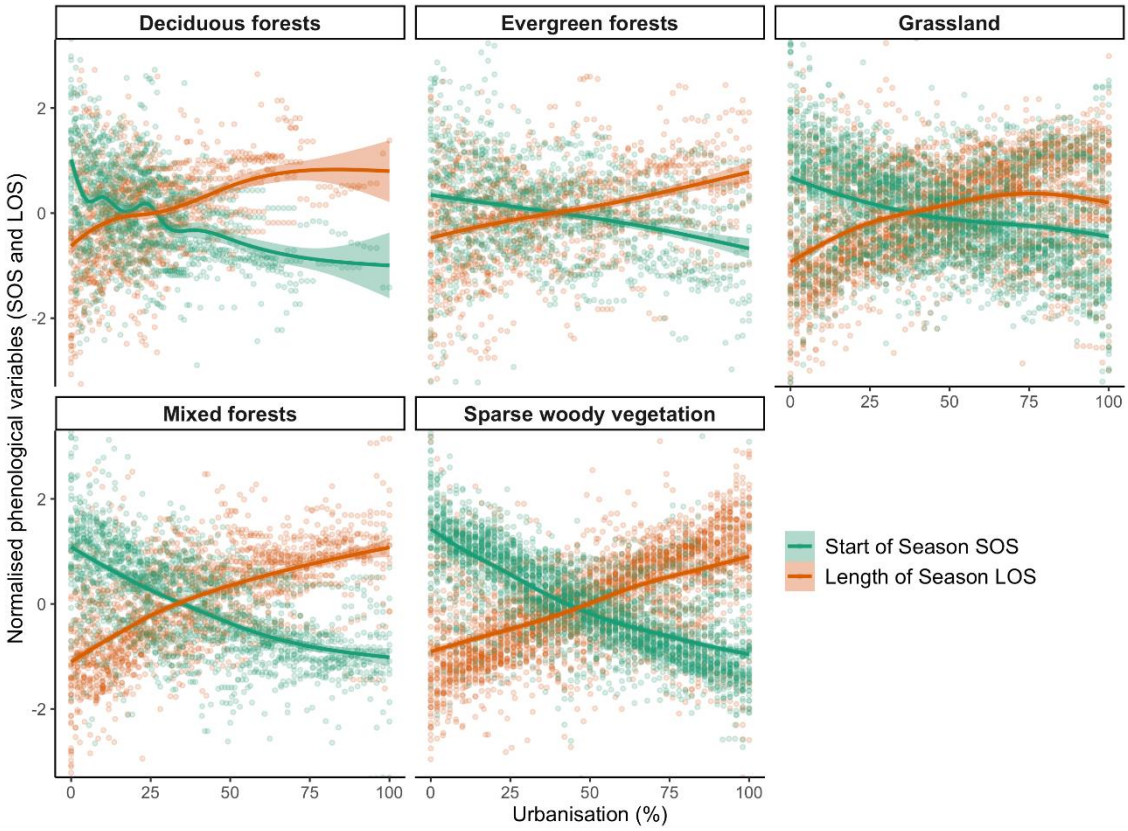


Figure 3. Phenological responses of the main vegetation types to urbanisation and time. (a) Phenological response to urbanisation intensity expressed as the regression coefficient of the linear relationship between the phenological indexes and the proportion of urbanised area (β_U^P). (b) Phenological shifts across the time series expressed as the regression coefficient of the linear relationship between the phenological indexes and year (β_Y^P). Elevation was included as a covariable. We only show significant values, i.e., points represent regression coefficients that were significantly different from zero.

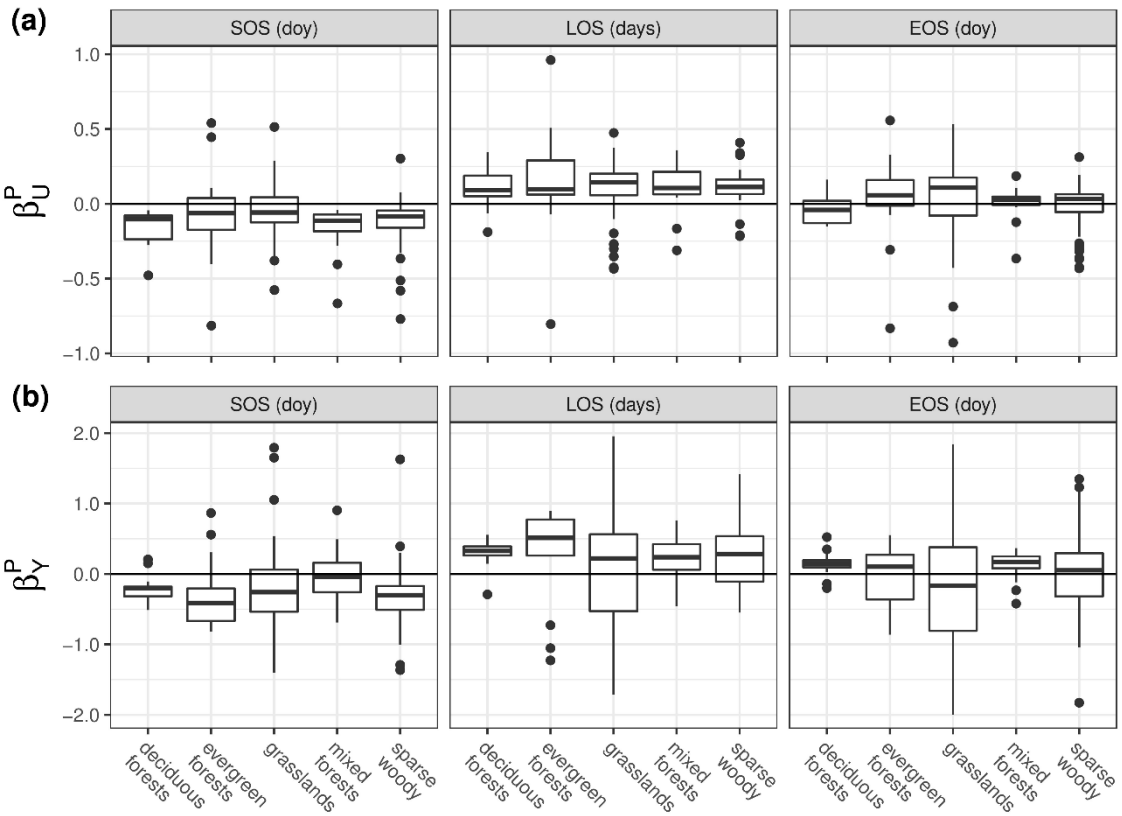


Figure 4. Variability of the phenological response of vegetation to urbanisation (β_U^P) across an annual mean temperature gradient. Colours indicate the macrobioclimate and symbols the main vegetation types. Bold solid lines represent significant linear regression patterns and dashed lines represent the 5 and 95 percentiles. SOS: start of season date, LOS: length of season in days, EOS: end of season date.

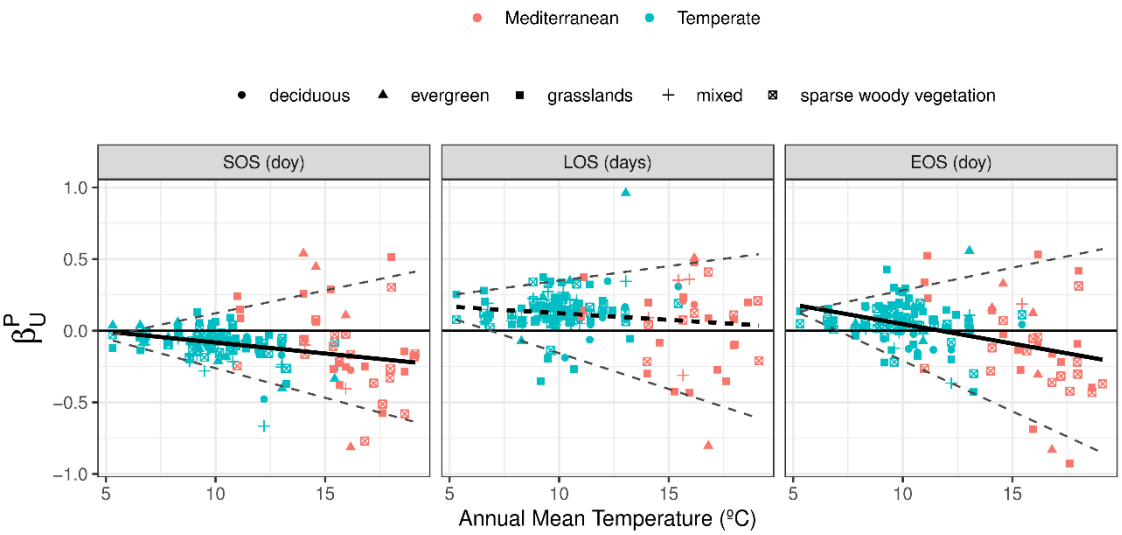


Figure 5. Phenological responses to urbanisation by the main vegetation types in metropolitan areas in the Mediterranean and Temperate macrobioclimates, expressed as the regression coefficient of the linear relationship between the phenological indexes and urbanisation intensity (β_U^P). Elevation was included as a covariable. We only show significant values, i.e., regression coefficients that were significantly different from zero.

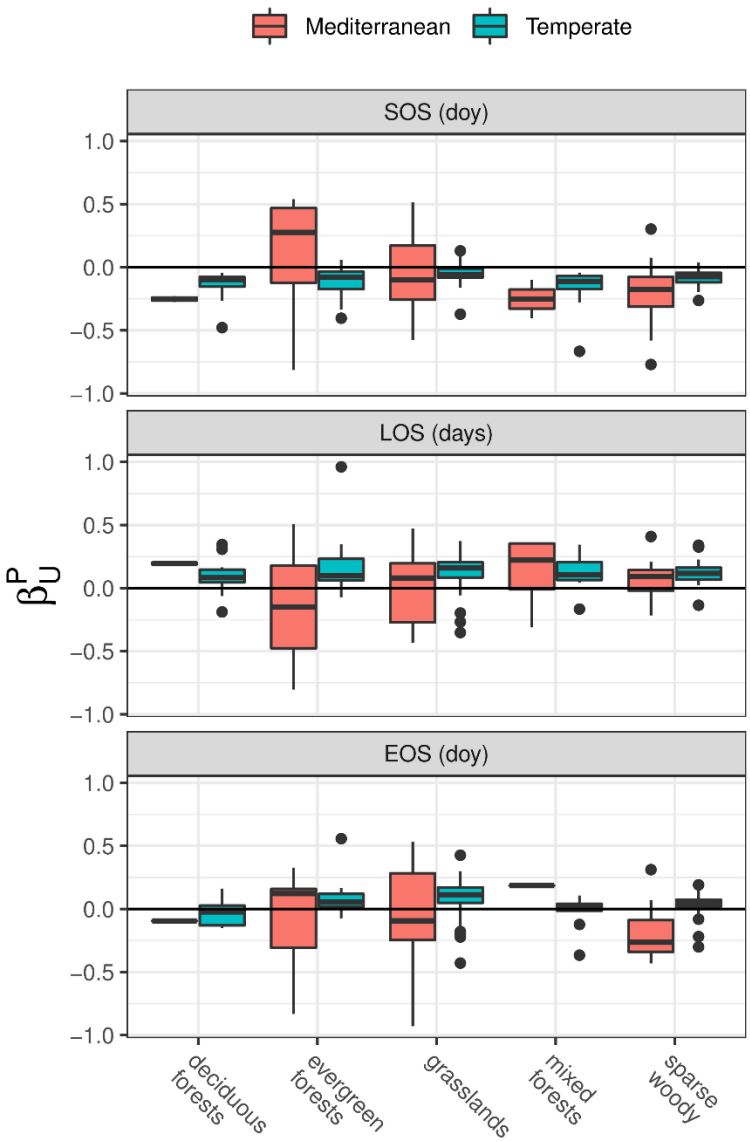
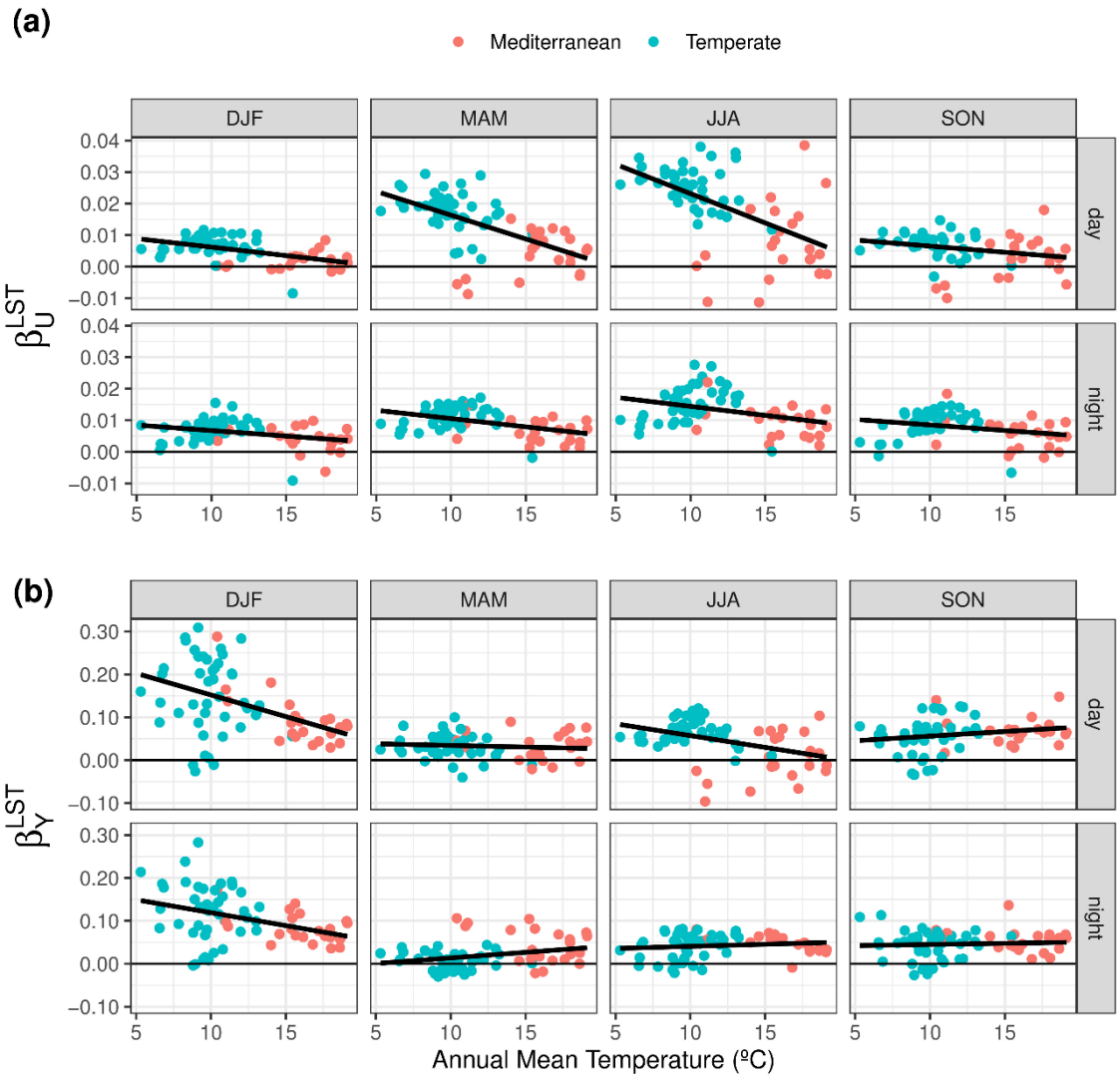


Figure 6. (a) Relationship between land surface temperature (LST) and urbanisation intensity (β_U^{LST}) for each metropolitan area, expressed as a function of annual mean temperature. (b) Relationship between the rate of increase of LST during the period 2002-2021 and annual mean temperature (β_Y^{LST}). Elevation was included as a covariable. DJF: winter, MAM: spring, JJA: summer, SON: autumn.



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