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The effects of climate change on the flowering phenology of alder trees in southwestern Europe

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Abstract. Global warming impacts plant phenology and the effect of climate change will be more intensely experienced at the edges of a plant's distribution. This work focuses on Iberian alder's climatic range (*Alnus lusitanica* Vít, Douda & Mandák). The Iberian Peninsula constitutes the Southwestern edge of the global chorological distribution of European black alder (*Alnus glutinosa* (L.) Gaertn. s.l.), and some of the warmest and driest conditions for the alder population are located in the center of Spain. The critical temperature-relevant periods that regulate the reproductive phenology of alder were analyzed using a statistical-based method for modeling chilling and forcing accumulation periods in temperate trees. Our results reveal that autumn chilling was the most important thermal accumulation period for alder in a Mediterranean climate while forcing requirements are satisfied in a short period of time. Autumn temperatures were significantly correlated with the timing of flowering, and chill units during this season directly influence start-dates of alder flowering. A positive trend was observed in pollen seasons' timing, meaning a slight delay of alder flowering in central Spain. It coincided with autumn warming during the period 2004-2018. If this warming trend continues, our results predict a delay in the start-date of flowering by around 3-days for every degree increase in maximum autumn temperatures according to the most optimistic emission scenarios.

Keywords. Phenology; Thermal requirements; Bioclimatology; Climate change; Alder; Mediterranean region

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Introduction

Climate change has multiple implications for biodiversity (Garcia *et al.*, 2014), as well as many other impacts on interconnected environmental domains (e.g., air, ecosystems, food, health, water, etc.) (Cramer *et al.*, 2018). The potential effects of climate change on plants are very diverse affecting individuals, species, and whole ecosystems (Fernández-González *et al.*, 2005). Increasing CO_2 concentrations and global temperatures may increase net primary productivity and extend the growing seasons (Donmez *et al.*, 2016). In some water-limited ecosystems, the effect of aridity has the opposite effect (Osborne *et al.*, 2000). Vegetation in areas with increasingly warmer and drier conditions will suffer changes in competitive interactions because plant species' drought tolerance determines plant survival to intense summer droughts and extreme heat events (García-Madrid *et al.*, 2016; Peñuelas *et al.*, 2001). Furthermore, global warming affects the timing of the main stages of plant life cycles from a phenological perspective (Picornell *et al.*, 2019; Rojo and Pérez-Badia, 2014).

Climate change in the Mediterranean basin has been revealed to be more dramatic than average worldwide changes during the 20th century (Guiot & Cramer, 2016). In the central Iberian Peninsula (Castilla-La Mancha region) annual mean temperatures have increased about 1.5 ºC during the last three decades (Gómez-Cantero *et al.*, 2018). However, warming is not homogeneous throughout the year, and summer and autumn are the seasons with the greatest increase in temperature concerning the mean values for previous climatological periods. The irregular distribution of precipitation has also marked recent decades. Most future climate scenarios forecast a decrease in rainfall and a generalized increase in the Mediterranean region's temperatures (Spanish Meteorological Agency, 2020).

Thermal requirements strongly regulate vegetative and reproductive plant development in deciduous forest tree species (Peaucelle *et al.*, 2019; Picornell *et al.*, 2019). The mid-latitudes climate is characterized by successive favorable and non-favorable periods related to a marked seasonality. In these climatic conditions, deciduous trees' dormant state is a physiological phenomenon related to frost tolerance and the protection of vegetative and

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reproductive tissues (Dewald & Steiner, 1986). During the dormancy period, the plant must achieve a certain level of chilling accumulation characterized by low temperatures. On the other hand, once chilling requirements have been reached, plants need to fulfill heat requirements (high temperatures) to initiate the plant development during the so-called forcing period *(*Luedeling *et al*., 2013). Warming negatively impacts chilling accumulation, and considerable reductions in chilling units have been documented across the Mediterranean region (Luedeling *et al*., 2011). It is especially worrying for Eurasian species like black alder, whose Mediterranean populations are located at the warmer edge of their distribution.

In Europe, the distribution of black alder (*Alnus glutinosa* (L.) Gaertn. s.l.) ranges from Scandinavia to the Mediterranean Basin along a wide ecological gradient characterized by a broad range of annual mean temperature and annual precipitation (Houston-Durrant *et al*., 2016) (Figure 1). Alder trees also cover parts of Asia, and this species was introduced in North America and Australia in the late 19th century (Kamocki *et al*., 2018). The plant is also present in central and southern parts of the Iberian Peninsula (and Northern Africa), where alder populations are considered to be at the edge of the European distribution of *A. glutinosa* s.l. (Pérez Latorre *et al*., 2011; Salazar *et al*., 2001), i.e., the most vulnerable alder populations to global environmental change (Lepais *et al*., 2013). Recent molecular and karyological studies recommend the disaggregation of alders of the Iberian Peninsula (except in the Pyrenees and Cantabrian Mountains) into a new species named *Alnus lusitanica* Vít, Douda & Mandák (Vít *et al*., 2017) (Figure 1).

Alder forests on the Iberian Peninsula are floodplain forests associated with periodically flooded riparian zones (Fernández-González *et al*., 2012). The alder forests have been classified separately at the level of alliance in the syntaxonomical classification system according to their biogeographical distribution (Rivas-Martínez *et al*., 2011): *Alnion incanae* for Eurosiberian and *Osmundo-Alnion* for Mediterranean forests. Recent classification studies confirm the strict Mediterranean character of the *Osmundo-Alnion* alliance (Biurrun *et al*., 2016). Alder forests are widely distributed in the North and western parts of the Iberian Peninsula (Douda *et al*., 2016) and are characterized by their ecological importance, provision of ecosystem services, and high conservation priority (Biurrun *et al*., 2016).

From the legal protection point, alder forests are included in the list of habitat types in the European Habitat Directive (Annex 1, Directive 92/43/EEC). In central Spain, this type of riparian habitat has been included in the Regional Catalogue of Special Protected Habitats of Castilla-La Mancha (Nature Protection Law 9/1999 of Castilla-La Mancha) (Martín-Herrero *et al*., 2003). Furthermore, *Alnus glutinosa* s.l. is also included in the Regional Catalogue of Protected Species of Castilla-La Mancha (Decree 33/1998).

This work focuses on the environmental ranges occupied by Iberian alder in the center of the Iberian Peninsula that, together with those located in southern areas of the Iberian Peninsula and Northern Africa, constitutes the edge of the global chorological distribution of European black alder. We hypothesize that alder populations located in the rear edge of the global distribution will be more affected by global warming than central populations, as supported by the Centre-Periphery Hypothesis (Pironon *et al*., 2017; Vilà-Cabrera *et al*., 2019), therefore significant changes will occur in the flowering phenology of alder trees in the central Iberian Peninsula. The main aims of this study are to: 1) Analyse the critical temperature-relevant periods that strongly regulate the reproductive phenology of alder trees in central Spain; 2) Study the current phenological changes occurring as a consequence of warming climate during recent years; 3) Predict potential changes to alder phenology if warming trends follow Representative Concentration Pathways proposed in the IPCC Fifth Assessment Report (Pachauri & Meyer, 2014).

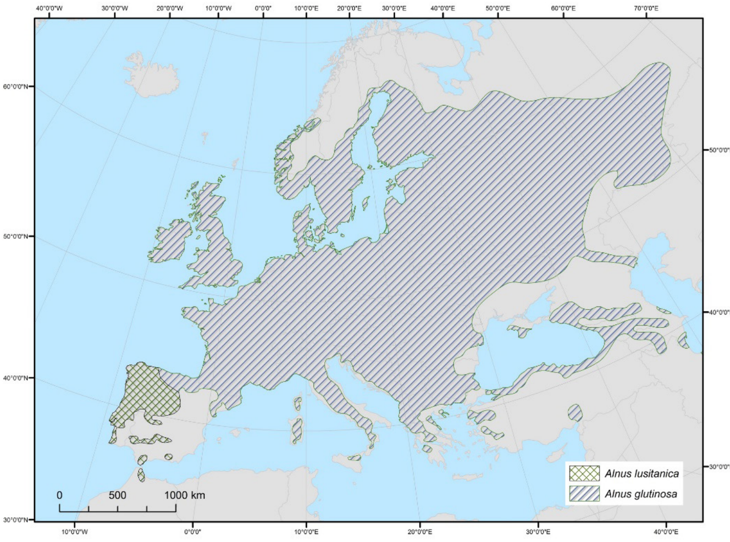

Figure 1. Geographical distribution of *Alnus glutinosa* s. str. in Europe according to the Chorological maps for the main European woody species (Caudullo *et al*., 2017), and approximate distribution of *A. lusitanica* according to the geographical information provided by Vít *et al*. (2017).

Material and Methods

Study area

In this study, we considered the alder forests of the Special Areas of Conservation (SAC) (Natura 2000 Network) located in the Northwest of the Castilla-La Mancha region: The northern SACs of Sierra de San Vicente (Central System), the Tiétar and Alberche river valleys (ES4250001, Code in the Natura 2000 Network) and the SAC Sotos del río Alberche (ES4250014); and the southern SACs of Montes de Toledo (ES4250005) and Tajo left margin rivers (ES4250013) (Figure 2).

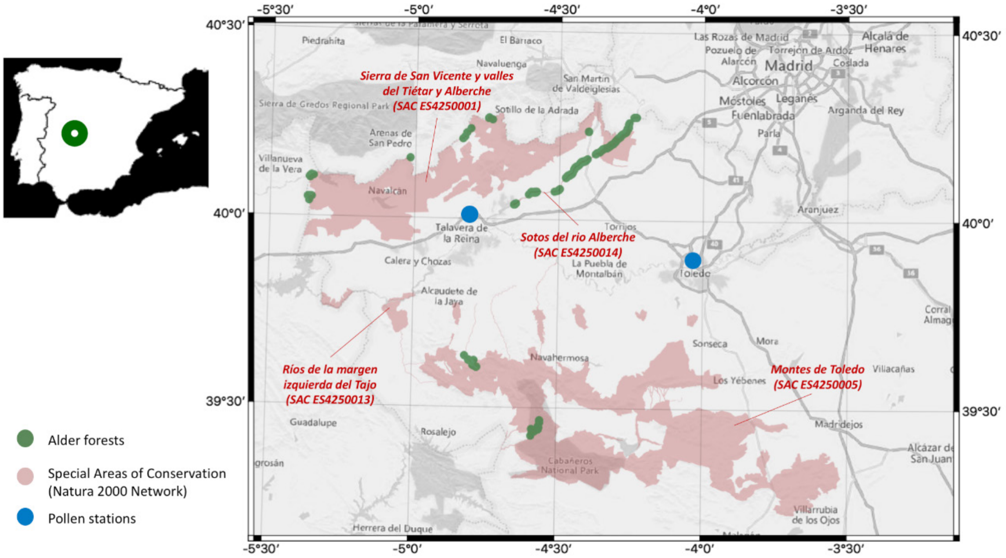

Figure 2. Location of the study area. Green points represent alder forests and red polygons, the study area belonging to the four Special Areas of Conservation (SACs) from the Network Natura 2000 in central Spain. Source of the base map: GoogleMaps ©.

The climate is characterized by two periods with the highest precipitation (autumn and spring) and a summer drought typical of Mediterranean climates. The annual precipitation in Montes de Toledo ranges from 500 to 1000 mm, decreasing to less than 400 mm in the bottom of the Tagus basin, and the annual mean temperature ranges from 10 to 14 ºC, reaching up to 16 ºC toward the Tagus valley (Ninyerola *et al.*, 2005). The annual precipitation of the northern SACs ranges from 500 mm in the lower valley of Alberche river to 600–1200 mm in the Sierra de San Vicente, and the mean temperature ranges from 11 to 17 ºC (Ninyerola *et al.*, 2005) (Figure 3A-B). Bioclimatically, the study area is characterized by a Mediterranean Pluviseasonal-Oceanic Bioclimate. Biogeographically, it is framed into the Mediterranean Iberian Occidental Province (Lusitan-Extremadurean Subprovince, Toledan-Taganean Sector) (Rivas-Martínez *et al.*, 2011).

Meteorological and climatic data

Different meteorological and climatic sources were used during this study. In the first step, climatic monthly data in the past (period 1951–1999) were used to characterise the climatic range where alder forests grow. For this purpose, we used a high-resolution climatic map as the digital climate atlas of the Iberian Peninsula (Ninyerola *et al.*, 2005), which has a grid cell size of 200 x 200 m.

Daily meteorological data (maximum, minimum, and average temperatures) were used during the period 2004–2018 for modelling of the alder phenology. In this case, meteorological datasets were provided by the Spanish Meteorological Agency in Spain (www.aemet.es). Finally, future projections of the models required applying the phenological models to the future. The last version of the WorldClim project was used (Fick & Hijmans, 2017). These climatic datasets were downscaled to 1x1 km of spatial resolution and a monthly temporal resolution.

Mapping of alder forests

The alder forests studied were mapped in detail at a 1:5000 scale. Vegetation mapping was carried out in vector format using QGIS 3.0 to delineate the polygons based on the high-resolution digital aerial orthophotographs provided by the Spanish National Aerial Orthophoto Program (PNOA) supported by the National Geographical Institute (www.ign.es). Mapping was completed with field campaigns to check the vegetation content of the polygons, including the presence of alder forests. The vector map has been rasterized using a grid cell size of 200 x 200 m. Then, the environmental range covered by the alder forests in central Spain was characterized with respect to the distribution of the Iberian alder (*Alnus lusitanica*). The occurrences of the alder tree (*A. glutinosa* s.l.) have been downloaded from the Global Biodiversity Information

Facility (GBIF) (www.gbif.org), only clipping the distribution area proposed by Vít *et al.* (2017) for *A. lusitanica* in the Iberian Peninsula.

Distribution of alder forests

Alder forests are well represented in the Alberche and Tiétar rivers, both tributaries of the right margin of the Tagus river in North (Figure 2). Alder trees grow sparsely in the Estena river and several streams in the Fresnedoso river's birth, all these areas located to the foothills of the Montes de Toledo. The number of occurrences (pixels of 200 x 200 m) of alder forests in the Alberche and Tiétar rivers was 138 points. In contrast, in the Estena and Fresnedoso rivers (Montes de Toledo) only 22 occurrences were identified (Figure 2). Alder forests in Montes de Toledo ranged from 550 to 950 m asl, and these forests grow in narrow water streams. On the other hand, alder trees in the Alberche and Tiétar rivers were studied in the middle of the rivers at an altitude of 300 to 500 m asl. These riparian habitats grow along wider rivers with higher flow regimes.

Alder trees in the study area of central Spain grow in a climatic range characterized by annual mean temperature ranging from 15 to 16 ºC, and annual precipitation of 500–1100 mm in Sierra de San Vicente (Alberche and Tiétar rivers). Conversely, alder trees in Montes de Toledo (Estena and Fresnedoso rivers) grow in areas with an annual mean temperature of 13–15 ºC and annual precipitation 400–800 mm. Figure 3C compares the local climatic range in the study area with the much broader environmental space occupied by *A. lusitanica* in the Iberian Peninsula.

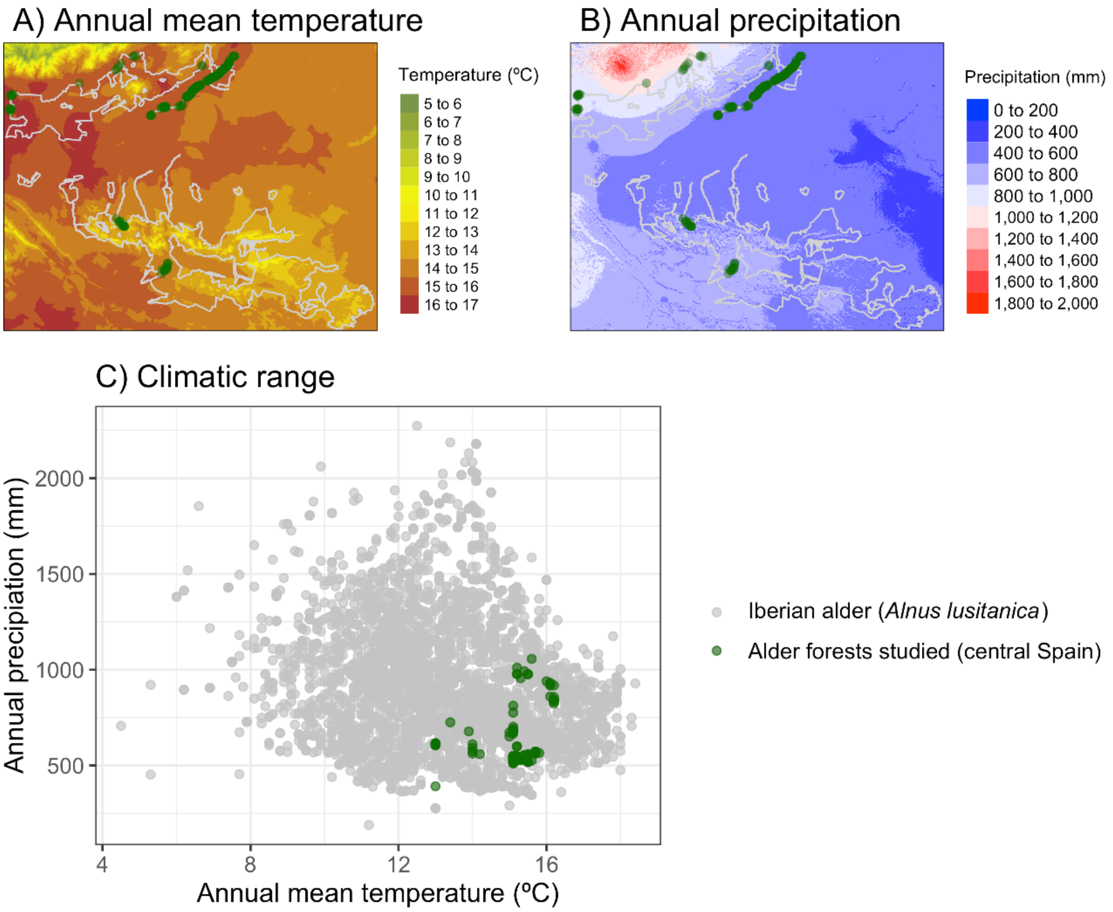

Figure 3. Annual mean temperature (ºC) and annual precipitation (mm) in the study area; A-B, climatic range of *A. lusitanica* (according to Vít *et al.*, 2017) in the Iberian Peninsula and occupied range in the study area (green points); C, source of the climatological data (Ninyerola *et al.*, 2005).

Phenological data

Phenological monitoring of alder forests located in the study area was based on an indirect methodology derived from airborne pollen sampling during the pollination period (hereafter flowering period). This procedure has been widely used in plant phenological studies from an ecological point of view (Dąbrowska & Kaszewski, 2012; Picornell *et al.*, 2019; Rojo *et al.*, 2018). Pollen seasons were defined using the 95% method, i.e., the pollen season's start-date occurred when 2.5% of annual pollen was collected, and the end-date of the pollen season occurred when 97.5% of the season's catch was reached. The peak-date was the day when the maximum pollen concentration was recorded every year. Phenological calculations were carried out using the AeRobiology R package, a specific tool for conducting aerobiological tasks (Rojo *et al.*, 2019).

Pollen monitoring was carried out in the city of Toledo during a 15-year period (2004–2018). The historical pollen time-series come from the dataset of the Aerobiological Network of Castilla-La Mancha of the University of Castilla-La Mancha (www.polencastillalamancha.com). In order to determine whether the long pollen time-series recorded in Toledo could be used in this study, the curve of airborne alder pollen recorded in Toledo was compared through linear correlation to the pollen curve recorded in Talavera de la Reina (a site situated close to the alder forests) during the period 2008–2013. A high correlation ($r = 0.71$, $p < 0.001$) indicates that although the pollen intensity could be different among stations, the pollen sources are the same and both stations could be used to calculate the timing of the pollen season (Skjøth *et al*., 2013). Trends of the phenological parameters (start, peak, and end-dates) were therefore calculated for the period 2004–2018 in Toledo using linear regression (slope) and Mann-Kendall test (tau).

Modeling

Start-dates of alder pollen seasons were correlated with monthly and seasonal temperatures recorded in the months before the beginning of the flowering period (from September of the previous year to January of the current year). Thermal accumulation periods were also defined in order to estimate chilling and heat requirements for alder flowering. For this purpose, we followed a statistical-based method proposed by Luedeling *et al*. (2013) to identify the critical temperature-relevant periods that influence the floral phenology of alder, and is widely used for other deciduous woody plants (Benmoussa *et al*., 2017; Martínez-Lüscher *et al*., 2016). Daily meteorological data (maximum, minimum and average temperatures) were used.

The detailed procedure to define the accumulation periods in this work is performed as follows: start-dates of alder flowering (response variable) were related to daily mean temperatures for each day from September of the previous year to the commencement of flowering (predictor variables). A moving average was applied to the daily temperature to ensure that the thermal periods were clearly recognizable (Luedeling & Gassner, 2012). The influence of temperature for each day on the timing of flowering was obtained from the results of Partial Least Square (PLS) regression, and the most relevant days were highlighted following the criterion of the Variable Importance in Projection (VIP) scores (Luedeling *et al*., 2013). In this case, the days reaching a VIP score of 0.8 were considered relevant days for alder's physiological thermal accumulation. Another important result of the PLS regression is the sign of the coefficients retrieved for the daily temperatures. Positive coefficients were related to chilling accumulation periods since the temperatures were positively correlated with the flowering dates. On the other hand, negative coefficients were related to heat accumulation periods (forcing period) since higher temperatures during this period were associated to an advance of the flowering dates. Potential thermal accumulation periods were estimated using the continuous periods of the PLS analysis results showing positive (chilling period) or negative (forcing period) coefficients.

The Dynamic Chilling Model was used to calculate chilling effectiveness units during the chilling accumulation period previously estimated (Fishman *et al*., 1987). This model assumes that chilling accumulation results from a first intermediate chilling product derived from low temperatures that can be converted into permanent chill units at low and moderate temperatures (Darbyshire *et al*., 2011). The equations of this model and the calculations of the thermal accumulation periods have been implemented for R software in the 'chillR' package (Luedeling *et al*., 2013).

Future projections

The results of the Partial Least Square regression analyses were used to construct a model relating the timing of flowering to temperatures recorded in the thermal accumulation periods previously estimated. The model was spatially applied to all points where alder forests grow in the study area using the current climatological data for 1970–2000 released in the last version of the WorldClim project (Fick & Hijmans, 2017). Finally, the phenological model was projected to the future for the periods 2050 (average for 2041–2060) and 2070 (average for 2061–2080) for several General Circulation Models (GCMs) used in the IPCC Fifth Assessment Report (Hijmans *et al*., 2005; Pachauri & Meyer, 2014), taking the potential radiative forcing as Representative Concentration Pathways (RCPs) 4.5 and 8.5 W/m^2 (van Vuuren *et al*., 2011).

Results

Flowering phenology of alder tree

In general, alder pollen seasons in central Spain occurred from mid-January (13th January ± 5 days of standard deviation) to late March (27th March ± 22 days). Therefore, start-dates of alder pollination occurred in a limited period from the 2^{nd} to 21^{st} January (2004–2018). Peak-dates usually occurred soon after the beginning of the pollination (30th January ± 9 days, Figure 4A). Clear positive trends were observed for the start, peak, and end-date of the alder pollination period (not significant), meaning there has been a slight delay in alder flowering in central Spain during the last 15 years. These results showed an averaged delay of 2.5 and 8 days every 10 years, respectively, to the start and peak-date of the alder pollen season (Figure 4B).

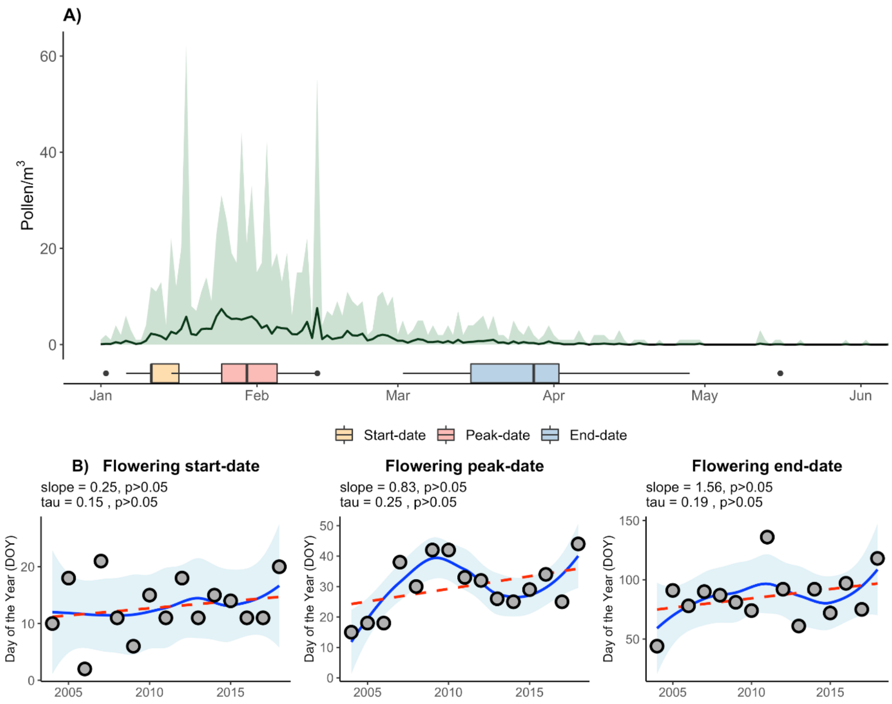

Figure 4. Amplitude (maximum and minimum) and mean values of the daily airborne pollen concentrations for the period 2004-2018. A, phenological graph of alder pollen; B, temporal trends of the main pollen season phenophases of alder (start, peak, and end-dates) for the period 2004–2018 using linear regressions (slope) and Mann-Kendall tests (tau).

Temperature-relevant periods for the initiation of flowering

The results showed a positive relationship between temperature during September-November (autumn) and the start-date of flowering in the next year (Table 1). The results coincide with those obtained from the PLS analysis reporting that the daily temperatures observed during the months September, October and November were positively correlated with flowering timing. In addition, these temperatures were important enough to be included as significant variables in the model of the start-date of the flowering (according to the VIP scores) (Figure 5A).

Table 1. Results of the Spearman correlation test among the start-date of the flowering of alder tree and average temperatures of the preceding months. Significance levels: * $p < 0.05$; ** $p < 0.01$.

Average temperature	Spearman corr.
September (preceding year)	0.60*
October (preceding year)	0.72**
November (preceding year)	0.53*
December (preceding year)	0.12
January	-0.04

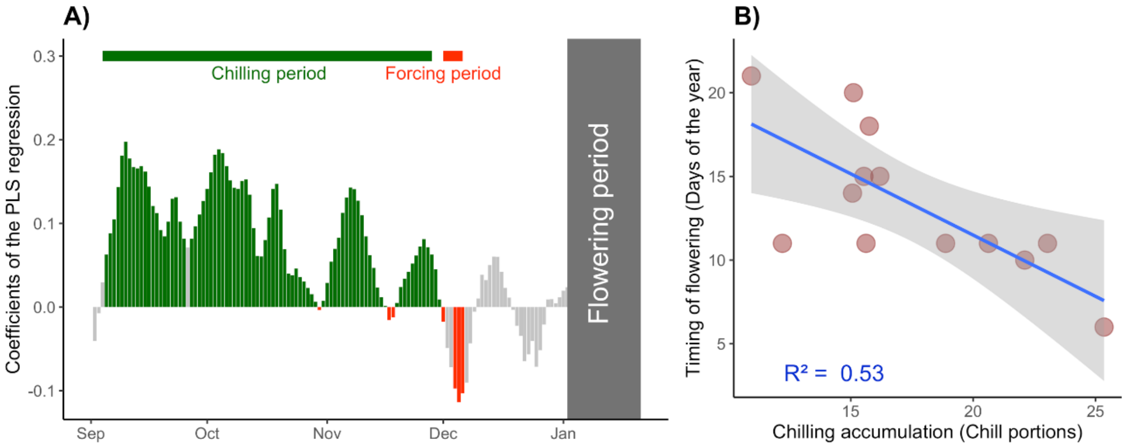

Figure 5. Identification of the chilling (green) and heat (red) accumulation periods following the modeling of the timing of flowering based on the PLS regression using A, daily mean temperatures as predictors, and B, the relationship between the timing of flowering and chilling units calculated during the autumn of the previous year (September-November) using the Dynamic model.

Positive coefficients of the PLS regression mean that during this period (September-November), the temperature has a direct relationship with the onset of the flowering period in alder trees (chilling accumulation period). The calculations derived from the Dynamic Chilling Model demonstrated that a lower accumulation of low temperatures (chilling process) was related to the delay of the timing of flowering of alder (Figure 5B).

The modeling results showed around a 3-day delay in the onset of the alder flowering for every degree increase in maximum temperatures during the autumn (mean for the three months September-October-November). Logarithmic models showed a stronger influence on the start of flowering than minimum temperatures (Figure 6A,B).

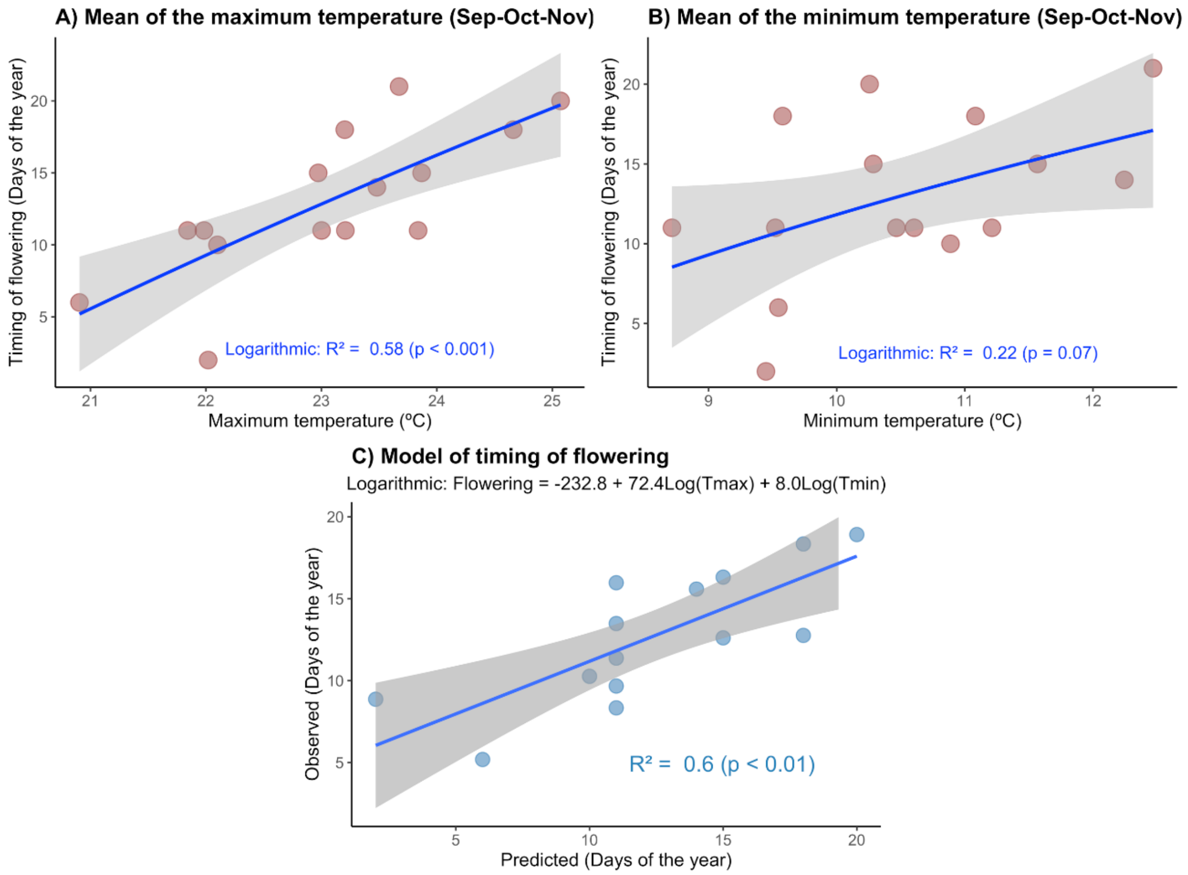

Figure 6. Relationship between the timing of flowering and average maximum and minimum temperatures during the autumn of the previous year (September-November) following a nonlinear model (logarithmic function). A, results of modeling the timing of flowering with mean maximum temperatures; B, results of modeling the timing of flowering with mean minimum temperatures; grey areas, 95% confidence interval; C, Non-linear (logarithmic function) models of alder flowering.

Future scenarios of flowering phenology

The model generated for the timing of alder flowering showed that all predictions result in a delay in alder pollen seasons under future climatic scenarios (Figure 7). The most optimistic scenario corresponds to INMCM4 General Circulation Models (GCM) with RCP 4.5, which forecasts an increase of about 2ºC in maximum autumn temperatures in 2070 (Figure 8). In the most pessimistic emission scenario GFDL−CM3 (RCP 8.5), autumn warming in the study area would be 4.5 and 7.5 ºC for minimum and maximum temperatures, respectively. Therefore, the average range of the phenological delay is predicted to be 6-27 days in the timing of flowering for 2070 compared to current conditions (about a 3-day delay per degree of increase in maximum autumn temperatures), considering both GCMs INMCM4 (RCP 4.5) and GFDL−CM3 (RCP 8.5), respectively (Figure 8). When the logarithmic model is applied, the most extreme phenological scenario (RCP 8.5) is slightly modulated for the 2070 period to a maximum delay of 25.5 days (Figure 8).

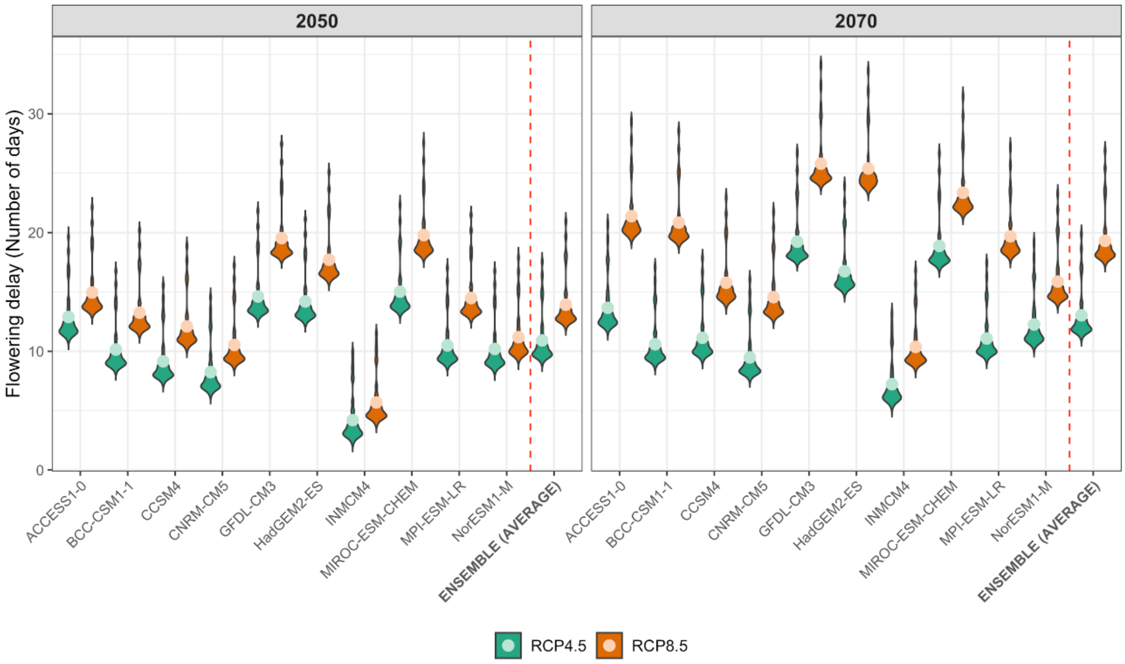

Figure 7. Potential phenological changes applying the logarithmic forecasting models based on the future climatic conditions projected by multiple General Circulation Models for RCPs 4.5. and 8.5. Points reflect the mean phenological changes for each GCM. The dashed red line indicate the Ensemble model calculated as average of the considered General Circulation Models.

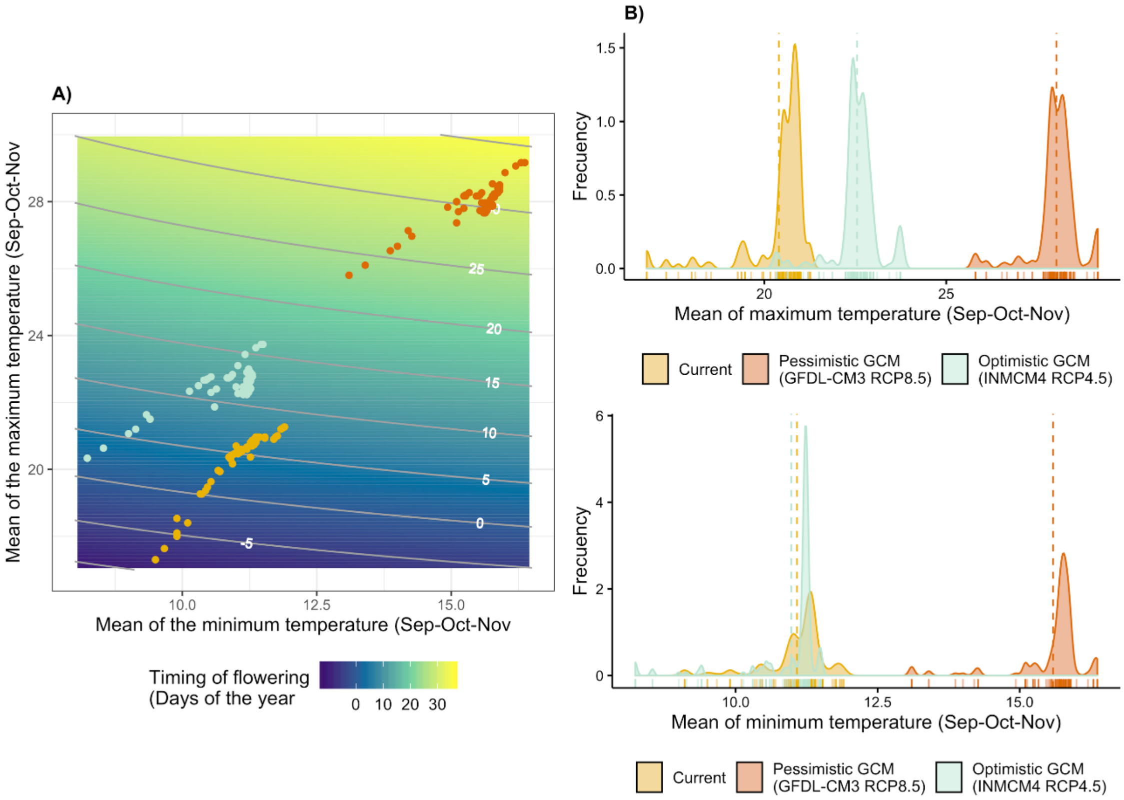

Figure 8. Future estimates based on the most optimistic and pessimistic emission scenarios according to the results of the Figure 6. A, changes to the timing of flowering; B, changes in maximum and minimum temperatures according to the selected General Circulation Models.

Discussion

The distribution of alder forests is limited by precipitation and temperature in Southern Europe, with aridity being one of the most important limiting factors for alder trees (Hemery *et al*., 2010). However, local precipitation rates in the areas where alder occurs is not particularly relevant since alder forest is a river flow dependent-vegetation and not directly rainfall dependent-vegetation. The head of the Alberche river is located in the Central System, a more humid area (annual precipitation 800−1000 mm) of about 1700 m asl. The periodic snow cover in the higher reaches of Alberche causes greater flow stability and high water availability throughout the year, which favors the development of the alder forests (Fernández-González *et al*., 2012). This is the reason for the wide ecological gradient and the fact that alder can grow even in dry parts of central and southern Spain (Pérez Latorre *et al*., 2011; Salazar *et al*., 2001). However, increasing aridity in upper river basins, as a consequence of climate change, would potentially trigger the reduction of alder tree distribution in the Mediterranean region (Attorre *et al*., 2011).

While the precipitation rate and aridity index are the main limiting factors for the distribution of alder, the temperature is the main factor influencing the seasonal life cycle of the black alder as well as other deciduous trees (Fu *et al*., 2019; Linkosalo *et al*., 2017; Picornell *et al*., 2019). The most important finding from our phenological modeling of alder flowering was the strong positive relationship between the timing of flowering and temperatures from the previous autumn. Moreover, a stronger effect was observed for maximum temperature during the chilling accumulation period of autumn than those retrieved by the minimum temperature. Therefore, the maximum temperature was more relevant for alder phenology than the minimum temperature as previously reported in Mediterranean plants (Gordo & Sanz, 2010).

A positive slope was observed for the timing of pollen seasons, meaning a slight delay of the entire pollen season of alder in central Spain during recent years. The warming of the autumn period could be an explanation for this phenological delay of alder trees. A significant trend was observed for monthly maximum October temperatures for the period 2004–2018 (slope = 0.24; $R^2 = 0.32$; $p < 0.05$), i.e. autumn temperatures have become warmer during recent years. Similar phenological trends were found in other Mediterranean areas of Southern Europe, such as Italy and the Iberian Peninsula, where a slight trend towards later start-dates of alder pollen seasons has been documented (Jato *et al*., 2013; Novara *et al*., 2016; Rodríguez-Rajo *et al*., 2011). On the other hand, these results contrasted with those from Central and Northwestern Europe (United Kingdom, Austria, Finland, Norway, Sweden, Iceland) (Emberlin *et al*., 2006; Jäger *et al*., 1996; Lind *et al*., 2016; Smith *et al*., 2014), all of which reported negative trends, i.e., alder flowering earlier over time. Our results contrasted with trends observed for other spring-flowering trees in the Mediterranean region that generally show an advance of the flowering period as a consequence of an increase of temperature during the forcing accumulation periods (García-Mozo *et al*., 2010; Gordo & Sanz, 2010).

Previous studies have noticed the importance of chilling accumulation for alder and other winter-flowering trees in the last autumn. The chilling phase has been identified as the most important thermal accumulation period for alder in the Mediterranean climate while forcing requirements are satisfied in a short period of time in alder trees of Southern Europe (González-Parrado *et al*., 2006; Novara *et al*., 2016). It supports the results of our study, but such behavior with respect to the thermal requirements may be different in other climatic conditions. Previous research based on thermal requirements conducted on alder in a temperate climate reported different findings with an increase in the importance of the heat requirements during the forcing period to alder budbreak (Emberlin *et al*., 2006; Malkiewicz *et al*., 2016).

Continentality and Thermicity indexes may play an important key role in the ecophysiology of alder trees associated with thermal requirements. Rodríguez-Rajo *et al*. (2006) documented significantly different chilling and forcing accumulations when very different bioclimatic areas, in terms of continentality and altitude, were compared in the boundary between Mediterranean and Eurosiberian biogeographical areas. Colder areas required greater chilling and forcing requirements since the trees need to be maintained in the dormant rest until the environmental conditions are suitable for plant development (Campoy *et al*., 2011; Lang, 1987). The flowering period of alder sequentially occurs following a continentality gradient from Southern Europe, Central and Northern Europe to Western Asia (Biedermann *et al*., 2019; Dąbrowska & Kaszewski, 2012; Jato *et al*., 2013; Kasprzyk, 2003; McVean, 1953; Turchina, 2019)

Bioclimatic triggers for changes in thermal accumulation periods and the phenological behaviour of alder trees in different bioclimatic areas are interesting topics for investigation (Dewald & Steiner, 1986). We hypothesize that the most critical temperature-relevant periods for alder in Mediterranean areas are the chilling phases that the tree must fulfill for bud break, and the achievements of chilling requirements may be threatened in the context of global warming (Chuine, 2010; Luedeling *et al*., 2011; Ma *et al*., 2018). On the contrary, in colder climates achieving chilling requirements during the autumn and winter would not be a limitation for the plant, forcing accumulation to become the most important thermal requirement (Rodríguez-Rajo *et al*., 2006). Further large-scale studies should be carried out that compare the reproductive phenology, and thermal requirements of black alder in different climate ranges using a unified modeling method. Also, considering the recent disaggregation of species in Europe and North

Africa (Vít *et al*., 2017), the ecophysiology of the different species should be studied and compared in the future.

All considered General Circulation Models (GCMs) predicted an increase in autumn temperatures in central Spain. From a phenological point of view, according to our results, alder flowering will be delayed by about 3-days for every degree increase in maximum autumn temperatures, but the response was not linear. We observed that a logarithmic pattern could reliably be used to relate the timing of flowering and environmental variables, and a nonlinear phenological trend was consistent with the data from the sampling period (Jochner *et al*., 2016; Morin *et al*., 2010). Adaptability to climate change, with declining rates of phenological change of the reproductive cycles, has been exhibited by several plants during recent decades (De Kort *et al*., 2016). Vegetative plant development has shown significant phenological changes during the last decades due to global warming (Morin *et al*., 2009). This fact may cause interference also in the reproductive cycle because both phases could overlap. In the same way as the flowering, alder trees showed advanced spring leaf unfolding to warming trends, although in this case, deciduous trees showed a nonlinear response (Fu *et al*., 2015).

Phenological changes have important consequences of planting survival. A reduction of the distribution area of alder may result from the limitation of the phenological plasticity of populations in the face of extreme environmental changes (Attorre *et al*., 2011; Turchina, 2019). Plant phenology is associated with the local adaptability of plant species to environmental conditions. Usually, flowering traits are genetically conserved by the populations, even those located in geographically distinct communities but occupying the same ecological niche (Chuine, 2010; De Kort *et al*., 2016; Thuiller *et al*., 2004). Moreover, phenology has relevance to the reproductive success of plants and the timing of flowering affects several phases of reproduction such as the pollination period, fruit set, fruit maturation and the quality of plant offspring, but other positive or negative coevolutionary processes are also very important such as those based on the phenological synchrony with herbivores, or pollinators and seed dispersers in other plants (Levin, 2006).

Other important changes in Mediterranean riparian vegetation would be those associated with the deterioration of habitat quality (Salinas *et al*., 2000). Such impacts would be magnified in marginal populations (Hampe & Petit, 2005). Compositional changes in vegetation are also found at the edge of the chorological areas (Rodríguez-Rojo & Fernández-González, 2014). Hydrogeological characteristics of Mediterranean river courses are expected to be altered by climate change, whose negative effects over riparian vegetation will be brought about by human management of river flows (Lytle *et al*., 2017; Palmer *et al*., 2008). In addition, climatic stresses may make riparian trees more susceptible to disease and speed up the decline of alder forests. Oomycete pathogens like *Phytophthora alni* Brasier and S.A. Kirk have already been associated with high mortality rates of alder trees in riparian ecosystems in Europe (Aguayo *et al*., 2014; Haque & Casero, 2012).

Riparian vegetation such as alder forests plays a key role in protecting riverbeds from an ecological point of view and providing important ecosystem services, especially in dry climates (González *et al*., 2017). Furthermore, marginal populations of alder located at the rear edge of alder distribution have a great biogeographical value. They have served as genetic sources to expand the temperate species over Europe after the Last Glacial Maximum of the Quaternary Era (Douda *et al*., 2014). High conservation priority is given to alder trees' Mediterranean populations because of their ecological and phylogenetic characteristics (Biurrun *et al*., 2016; Lepais *et al*., 2013).

Conclusions

Advances in the timing of flowering of forest tree species due to increasing temperatures during the forcing period have been documented in recent decades. However, in some species whose chilling period is becoming more and more relevant, the phenological response may be different as in the case of alder in the Iberian Peninsula center. Alder is a winter-flowering species whose onset of the flowering period normally occurs during January, and so the chilling accumulation period is crucial for achieving suitable reproductive development. It is, in part, a consequence of being part of the rear edge of the ecological gradient of the species, which makes the population in central Spain extremely vulnerable to climatic warming. If the current trends of phenological traits continue over time, the flowering period of Iberian alder (*Alnus lusitanica*) will experience a considerable delay of around 3 days per degree of increase in maximum autumn temperatures according to the most optimistic emission scenarios. Other potential changes, caused by increasing aridity or greater irregularity in precipitation projected for the Mediterranean Basin, are associated with a reduction in the potential ecological niche of alder and the deterioration of the structure and floristic composition of Iberian alder forests.

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