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Research article

Phenology in winter-deciduous relict Mediterranean forests as a tool to understand their adaptation to climatic seasonal cycles

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Winter deciduous forests signify a relict ecosystem that survives restricted to microclimatic zones of high mountains in the western Mediterranean Basin and they are well represented in the southern Iberian Peninsula (Sierra Nevada, Spain). Given the scarce knowledge of their phenological behaviour, the aim of this work was to obtain the annual phenophasic sequencing and phenophasic indexes, at both species and plant community level and to determine its phenological functional groups (FG). Phenophase sequencing, phenophasic patterns and indexes have been determined considering the winter functionality of most species. As methodology was initially implemented for typically Mediterranean vegetation, new vegetatives and reproductives phenophases have been proposed. The majority of the studied taxa showed their activity concentrated between April and June, coinciding with the rise in temperatures and when rainfall is maintained, while winter is generally a non-phenophasic activity season mainly due to low temperatures and frequent frosts. The annual phenophasic characterisation of the forest and its comparison with other Mediterranean ecosystems highlighted that the maximum vegetative phenophasic activity occurs in spring, as do evergreen forests. In contrast, the maximum reproductive activity takes place between spring and early autumn but, in evergreens, it occurs throughout the year. The maximum active phenophasic period of the plant (APS) was achieved in spring due to optimal environmental conditions in terms of temperature and humidity, while the minimum values were achieved from late autumn through late winter (December, January and February) due to unfavourable environmental conditions. In the deciduous forest, the phenophasic duration of reproductive functions predominated over vegetative functions and this is typical of Mediterranean forests and mainly of deciduous tree species. Four functional groups were identified: FG1 – early and prolonged foliation and dispersal; FG2 – very short dispersal and fructification; FG3 – very long-lasting foliation and fruiting, FG4 – long foliation.

Keywords: bioclimate, functional groups, phenophases, Sierra Nevada National Park, submediterranean forest

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Introduction

Phenology deals with the study of the seasonal cyclical activity of plants and biological life cycle (Nadia et al. 2014) and has traditionally been carried out by monitoring species through direct observation in the wild or more recently through satellite observation (Menzel 2000, Ahas et al. 2002, Rodriguez-Galiano et al. 2015).

Phenological science is fundamental to understanding ecological interactions between natural systems (Denny et al. 2014) and is currently of particular relevance to evaluate the impact of climate change on the phenological phases occurring in plant organs (Denney and Anderson 2020, Montgomery et al. 2020, Meier and Bigler 2023). To know the trend of phenological changes in vegetation is of crucial importance for understanding their adaptations in response to climate change (Jiao et al. 2020). Global temperature has increased by approximately 1°C since pre-industrial times, most dramatically in the Mediterranean basin by 1.3°C (Guiot and Cramer 2016, IPCC 2021) which is phenologically affecting many taxa (Parmesan 2006, Cleland et al. 2007, Thackeray et al. 2010) and overall ecosystem functioning (Menzel 2002, Keenan et al. 2014, Picornell et al. 2019, 2023, Rojo et al. 2021), most noticeably in Mediterranean mountainous areas of southern Europe such as Sierra Nevada (Rondinel-Mendoza et al. 2024).

Among the phenological methods used to characterise plant communities in Mediterranean ecosystems, the method developed by Orshan (1989) stands out. It studies the effect of seasonal changes on plant organs during their annual cycle. This method, which is mainly applied in regions of the planet with a predominantly Mediterranean climate (Floret et al. 1987, 1990, Romane 1987, Montenegro et al. 1989, Danin and Orshan 1990, Keshet et al. 1990, Le Roux et al. 2014, Spano et al. 2024) has been applied in the Iberian Peninsula and in large areas of the Mediterranean Basin, especially in ecosystems formed by scrublands and forests adapted to summer aridity, where taxa respond phenologically to dryness with the total or partial loss of their leaves (Pérez-Latorre et al. 1996, 2007, 2009, Castro-Díez and Montserrat-Martí 1998, Guàrdia-Rúbies et al. 1998, Navarro and Cabezudo 1998, Pérez-Latorre and Cabezudo 2002, 2006, Milla et al. 2010, Hidalgo-Triana and Pérez-Latorre 2018, 2019, 2021). In the Mediterranean region and within the Mediterranean macroclimate, relict temperate-deciduous forests (Heberling and Muzika 2023) can be found from interglacial and finiglacial periods, transition phase between the end of the last glaciation (Pleistocene) and the beginning of the present climate (Holocene), that were colder and wetter than the present (Blanca 2000). These relict temperate forests are located in refuge areas because the current summer dry, Mediterranean climate, does not correspond to their origin and they could be the most affected by climatic changes towards greater aridity and higher temperatures (Petit et al. 2005), which could lead to a decrease in their area of distribution or even their disappearance (Bakkenes et al. 2002, Sánchez de Dios et al. 2009, 2019). Studies on this type of temperate-deciduous forest are important for its conservation (Blanca-López and López-Onieva 2002), even more so in the western Mediterranean area of Europe, where these habitats are protected by the European Directive 92/43 EU Annex I (www.boe.es/buscar/doc.php?%20id=DOUE-L-1992-81200). A good representation of this type of deciduous forests is currently found in the Sierra Nevada National Park (southern Iberian Peninsula, Spain) where they are considered as relicts and require cooler and wetter climatic conditions than the current ones, so they are located in microclimatic zones that are locally suitable for their persistence (i.e. a restricted habitat), but they are very sensitive to any environmental disturbance, so their conservation is a priority (Bonet et al. 2011, Blanca et al. 2019).

This type of forest presents several functional and phenological adaptive peculiarities that contrast with Mediterranean evergreen vegetation, one of which is the winter fall of the leaf canopy (Montserrat-Martí et al. 2004). This fact determines a different phenophasic behavior to be studied, being a phenophase the identifiable stage in the life cycle mainly in plants that is influenced by environmental factors. Another tool for understanding the adaptation of groups of species in ecosystems to the environment in which they live is the study of functional groups (FG), which are groups of taxa that show similar responses to environmental conditions and appropriate to exercise a common management on them (Herrera 1984, Walker 1992, 1995, Noble and Gitay 1996. Díaz and Cabido 1997, Boulangeat et al. 2012, Hidalgo-Triana et al. 2023). Just as phenophases provide information on the annual cycle of a plant community, the determination of phenological functional groups provides a reduction in the complexity of plant ecosystem functioning at the species level (Walker 1992, Grime et al. 1997) and can be used to assess ecosystem functionality (Gitay and Noble 1997).This proposed groups are still unknown for the kind of studied forests in this work.

As phenological activity is of great importance to understand the adaptation of plants and vegetation to their environment and these data have not yet been obtained for relict deciduous forests in Mediterranean bioclimate environments, the present research study proposes, using the phenophasical methodology, the following objectives: 1) to obtain the annual phenophase sequencing for the species that constitute the forest and to obtain their phenophasic indices; 2) to obtain the annual phenophase sequencing and phenophase indices at the community level; and finally, 3) to identify phenologically based functional groups.

Material and methods

Study area

This study was conducted in the northern slope of Sierra Nevada National Park, on the upper basin of the Alhama de Lugros River (Lugros municipality, Granada province, Andalusia, Spain; Fig. 1), with an extension of approximate 7 km^2 and altitudes between 1450–1800 m a.s.l. This zone

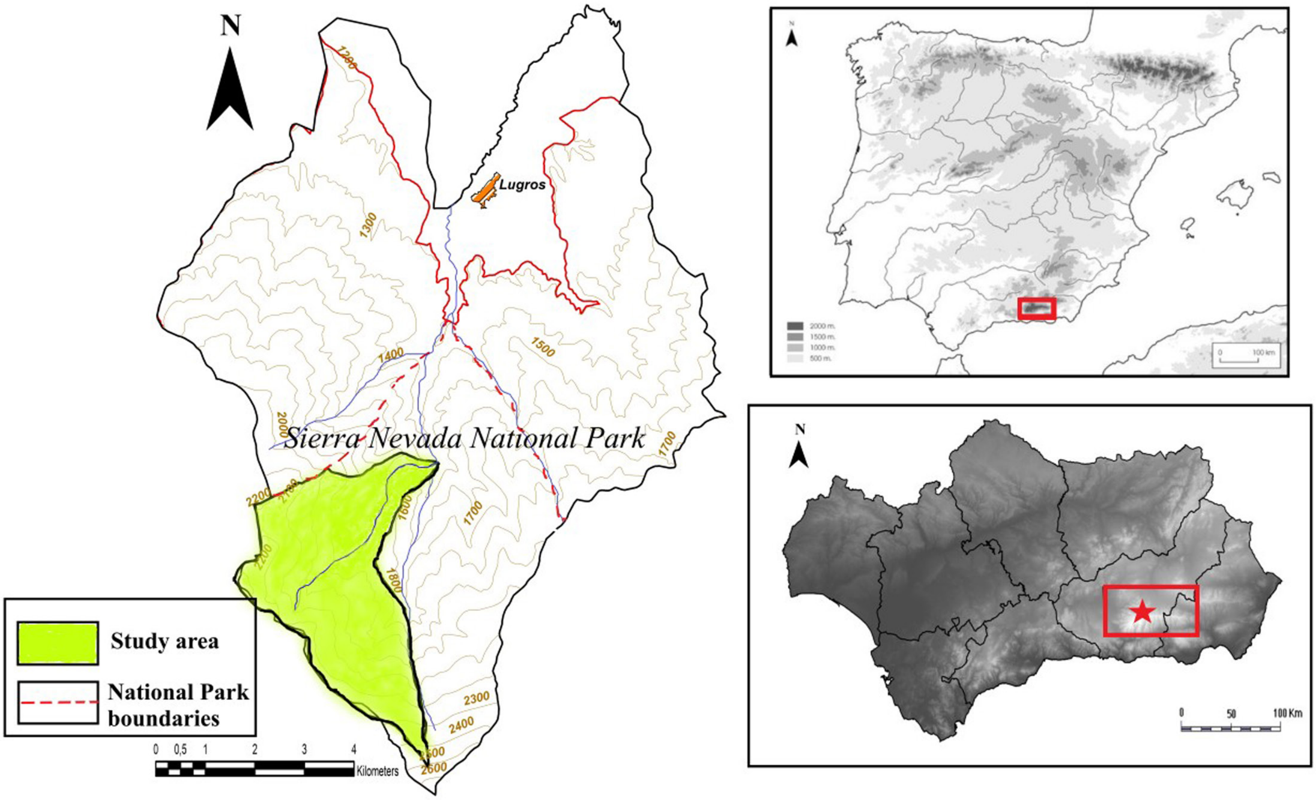

Figure 1. Location of the study site. Red rectangle in the Iberian Peninsula. Red star in Andalusia (Spain). Detailed map in the northern face of Sierra Nevada National Park.

has a siliceous lithological composition, predominantly of micaschists and quartzites, belonging mainly to the Nevado-Filabride geological complex (Martín et al. 2008); soils mainly correspond to regosols and luvisols, forest soils with a sandy loam texture and a pH close to neutral with a slight tendency towards acidic (De Pedraza-Gilsanz 1996).

In order to characterize from a bioclimatic point of view the studied area, bioclimatic parameters and indexes have been calculated (Rivas-Martínez 2007, 2011, 2017) based on the data obtained during the years 2008–2019 (Supporting information) from the two meteorological stations present in the territory. Embarcadero weather station (37°11′N, 03°15′W) is located in the lower area of the studied territory at an altitude of 1517 m and Piedra de los Soldados weather station (37°09′N, 03°15′W) is located in the upper area, at an altitude of 2155 m. In territories where there is a transition between the Mediterranean and Temperate climates, the Sub-Mediterranean variant is considered and measurable with the submediterraneity index (Loidi 2017).The submediterraneity index was determined for both stations (Supporting information). As a result, the thermotype lower supramediterranean (mean annual temperature $T = 12.38°C$; compensated thermal index; $Itc = 219$) and the ombrotype lower subhumid (average annual rainfall $p = 540.15$ mm; annual ombrothermic index $Io = 4.89$) were identified. Moreover, a submediterranean level between 1–30 was calculated, which means that the study area shows an extremely weak submediterranean level. The bioclimatic data can be found in the Supporting information.

Biogeographically, the area is ascribed to the Nevadense District, in the Nevadense Sector of the Sierra Nevada Mountain range geographical area, inthe Baetic province, in the southern Iberian area of the Mediterranean region (Marfil et al. 2017).

Studied species

Eighteen species were selected (Table 1, Supporting information) as a representative sample of the plant composition of the mixed winter-deciduous forests (Heberling and Muzika 2023) of Sierra Nevada. These species are part of both the tree layer and the shrub mantle layer (Martínez-Parras and Molero-Mesa 1982, Molero-Mesa and Marfil 2017). Selected species were acquired from representative phytosociological inventories which were carried out in the areas of the mixed deciduous forest (Supporting information) following the Braun-Blanquet (1979) methodology. Among the studied species, most were tree species (i.e. mesophanerophytes) and shrubby species (i.e. nano- and microphanerophytes; Raunkiaer 1905, Orshan 1986, Blanca et al. 2011, Table 1). In addition, the biological type according to Blanca et al. (2011) and leaf type according to Orshan (1986) were also included in the study. For each studied species, we collected herbarium sheets and deposited them in the Herbarium of

Table 1. List of studied species (Meph: mesophanerophytes. Miph: microphanerophyte. Nph: nanophanerophytes), (Malacophyll: slightly fleshy leaves. Sclerophyll: hard leaves) according to Raunkiaer (1905), Orshan (1986) and Blanca et al. (2011).

Species	Family	Biological type	Leaf type
Acer opalus Mill. subsp. *granatense* (Boiss.) Font Quer & Rothm	*Aceraceae*	Meph.deciduous	Malacophyll
Berberis hispanica Boiss. & Reut.	*Berberidaceae*	Naph.deciduous	Malacophyll
Betula pendula Roth subsp. *fontqueri* (Rothm.) G.Moreno & Peinado	*Betulaceae*	Meph.deciduous	Malacophyll
Lonicera arborea Boiss.	*Caprifoliaceae*	Miph.deciduous	Malacophyll
Quercus pyrenaica Willd.	*Fagaceae*	Meph.deciduous	Malacophyll
Quercus x trabutii Hy.	*Fagaceae*	Meph.deciduous	Malacophyll
Fraxinus excelsior L.	*Oleaceae*	Meph.deciduous	Malacophyll
Rhamnus cathartica L.	*Rhamnaceae*	Miph.deciduous	Malacophyll
Prunus avium L.	*Rosaceae*	Meph.deciduous	Malacophyll
Malus sylvestris (L.) Mill.	*Rosaceae*	Meph.deciduous	Malacophyll
Rosa corymbifera Borkh**.**	*Rosaceae*	Miph.deciduous	Malacophyll
Cotoneaster granatense Boiss.	*Rosaceae*	Miph.deciduous	Malacophyll
Crataegus granatense Boiss.	*Rosaceae*	Miph.deciduous	Malacophyll
Prunus ramburii Boiss.	*Rosaceae*	Naph.deciduous	Malacophyll
Sorbus aria (L.) Crantz	*Rosaceae*	Meph.deciduous	Malacophyll
Sorbus hybrida L.	*Rosaceae*	Miph.deciduous	Malacophyll
Salix caprea L.	*Salicaceae*	Meph.deciduous	Malacophyll
Taxus baccata L.	*Taxaceae*	Meph. evergreen	Sclerophyll

the University of Malaga [MGC] and made them available in the global biodiversity information facility (GBIF 2023). The Vascular Flora of Eastern Andalusia (Blanca et al. 2011) and the Iberian Flora (Castroviejo et al. 1986–2021) were used to identify the taxa. Nomenclature and taxonomy (i.e. family) follows Blanca et al. (2011).

From a phytosociological-syntaxonomical point of view, the studied vegetation corresponds to a winter deciduous forest of *Quercus pyrenaica*, accompanied by other broadleaved species, which develop on shady slopes and temporihygrophilous soils in the supramediterranean subhumid thermotype belonging to the phytosociological sub-association (*Adenocarpo decorticantis–Quercetum pyrenaicae aceretosum granatensis* Martínez-Parras and Molero-Mesa 1982, class *Querco–Fagetea* Br.- Bl. and Vlieger in Vlieger 1937). The phytosociological data can be found in the Supporting information.

Phenophasic sequencing, patterns and indexes

Ten adult individuals of each of the 18 species, from well-preserved environments, were selected for this phenological study (Cornelissen et al. 2003). In case of a low density of individuals in the population, we considered fewer than 10 individuals (Pérez-Harguindeguy et al. 2013). Sampling was carried out over a period of one year, between March 2019 and February 2020. Monitoring was conducted around the 15th of each month to represent the entire month. The method used for the phenological study followed Orshan (1989), which was developed for mediterranean species although with modifications and updates (Pérez-Latorre and Cabezudo 2002, Milla et al. 2010, Hidalgo-Triana and Pérez-Latorre 2018).

The presence or absence of phenophases and subphenophases (more precise divisions within a main phenophase) belonging to each of the selected species was recorded in monthly field sampling individuals, where each vegetative and reproductive phenophase and subphenophase was noted in percent and numerical intervals of activity,considering an active phenophase that occurred in at least 5% of the individuals; otherwise, it was considered an infrequent event (Castro-Díez and Montserrat-Martí 1998, Castro-Díez et al. 2003). Photographs and/or organs of the plantin phenophasic states were taken each sampling time.

New updates were made in this work, due to the winter-deciduous functionality of the major part of the species. One update is the proposal of two new types of species as an addition to the existing types according to their response to summer drought (arid-active and arid-passive ones: 1) cryo-active species which remain photosynthetically active in the cold season (i.e. evergreen species), and 2) cryo-passives which remain in vegetative photosynthetic stand still in the winter (i.e. winter deciduous species).

The different studied phenophases were divided into vegetative and reproductive phenophases. The vegetative were: Dolichoblast Vegetative Growth -DVG- (with updates of the methodology as two new subphenophases as bud formation -DVGbf- and Formed Stable Buds -DVGfsb-) and Brachyblast Vegetative Growth -BVG- (dolichoblast refers to a type of branch with elongated growth and brachyblast a type of branch with shorter growth). A new phenophase of Leaf Activity -LA- with two new subphenophasesas Young Leaves -LAy and Adult Green Leaves -LAag-has been set. A new phenophase of Leaves Fallen on the Ground -FLG- has been established, which represents the monthly presence of newly fallen leaves on the ground, generally in autumn. Leaf senescence (LS) is defined as the monthly presence of senescent leaves on the canopy. Phenophases were measured as follows: DVG as length (cm) of branch elongation with juvenile leaves; DVGbf as presence of buds in their juvenile size; DVGfsb as presence of buds in their adult size, BVG as length (cm) of branch elongation with juvenile leaves, LA as presence of photosynthetic leaves; LAy as presence of juvenile leaves; LAag as percentage of presence of adult photosynthetic leaves in the canopy; FLG as presence of fallen leaves in the base of the plant; LS as percentage of senescent leaves in the canopy.

The studied reproductive phenophases were: flower bud formation (FBF), flowering (F) and fruit set (FS) with three new subphenophases (growth -FSg-, colour change -FSc-and ripe -FSr-), and seed dispersal (SD). The F and FS phenophases were measured as percentages of the canopy occupied by the phenophase (Denny et al. 2014). Phenophases were measured as follows: FBF as presence and percentage of presenceof flower buds; F as presence and percentage of presence of flowers in the canopy; FS as presence of fruit; FSg as presence of fruits growing (normally green); FSs as presence of fruits changing colour (normally towards orange or yellow); FSr as presence of fruit completely mature (normally red, brown or purple).

Phenophasic indexes and patterns were calculated for each species:APS (active phenophasic period of the species), RVA (species reproductive/vegetative activity), PSI (phenophase sequence index), PPT (species phenophasic pattern) (Castro-Díez and Monserrat-Martí 1998, Pérez-Latorre and Cabezudo 2002, Hidalgo-Triana and Pérez-Latorre 2018, Paul et al. 2018) (Supporting information).

Three new phenophasic indexes are defined in this work:

1. ‘Index of leaf activity/senescence of the species’ (LAS):

$$\frac{\text{sum of months with photosynthetic activity} \begin{bmatrix} \text{LA young leaves}\left(\text{LAy}\right) \\ +\text{LA adult leaves formed}\left(\text{LAag}\right) \end{bmatrix}}{\text{number of months with leaf senescence}\left(\text{LS}\right).}$$

This index takes values between 1.5–6.0. Species with a low LAS value would show a higher efficiency to a short photoperiod and to cold and long winters. Conversely, a high LAS value indicates an adaptation to a long photoperiod and mild temperatures most of the year (Table 3).

2. ‘Phenophasic index of fallen leaves on the ground’ (LGI):

This index is defined as the number of months of the annual phenophasic cycle with newly fallen leaves under the canopy. Low LGI values ($\text{LGI} \leq 3$) correspond to deciduous species, and high values ($\text{LGI} \geq 4$) represent marcescent species, deciduous species that retain all or part of senesced leaves on branches through much of winter (Heberling and Muzika 2023). Leaf senescence (LS) would divide species into deciduous and marcescent.

$$\frac{\text{sum of months with LA activity; } t\left(\text{LA}\right)}{\text{sum of months with LS activity; } t\left(\text{LS}\right)}$$

3. ‘Flowering and growth overlapping index’ (FGi), which represents:

$$\frac{\text{sum of months with overlap} \\ \text{between vegetative growth}\left(\text{DVG}\right) \\ \text{and flowering}\left(\text{F}\right);t\left(\text{DVG+F}\right)}{\text{sum of months without} \\ \text{overlap; } t\left(\text{DVG}\right)+t\left(\text{F}\right):}$$

Where ‘t’ is the number of months necessary to complete the phenophases represented in parentheses. Index values close to one indicate that the phenophases are highly overlapping, while index values close to zero indicate sequential of the

Table 2. Variables used in the PCA and in the cluster analysis.

Variable		Abbreviation classes in the matrix
Abbreviation classes in the matrix (no. of buds growing)	FBF_1	0–365 number of days per year with phenophasic activity
Flower bud formation (percentage of stable formed buds)	FBF_2	0–365 number of days per year with phenophase activity
Flowering (no. of flowers)	F	0–365 number of days per year with phenophase activity
Fructification (fruit growth)	FS_1	0–365 number of days per year with phenophase activity
Fructification (colour change)	FS_2	0–365 number of days per year with phenophase activity
Fructification (mature fruit)	FS_3	0–365 number of days per year with phenophase activity
Seed dispersal (no. of fruits per square meter)	SD	0–365 number of days per year with phenophase activity
Vegetative growth (percentage of buds forming)	VG_1	0–365 number of days per year with phenophase activity
Vegetative growth (percentage of stable formed buds)	VG_2	0–365 number of days per year with phenophase activity
Vegetative growth of the dolichoblast (elongation in centimeters)	DVG	0–365 number of days per year with phenophase activity
Leaf activity (percentage of young leaves)	LA_1	0–365 number of days per year with phenophase activity
Leaf activity (adult green leaves)	LA_2	0–365 number of days per year with phenophase activity
Leaf senescence (percentage of discoloured leaves)	LS_1	0–365 number of days per year with phenophase activity
Leaf senescence (percentage of marcescent leaves)	LS_2	0–365 number of days per year with phenophase activity
Leaf senescence (percentage of leaves falling)	LS_3	0–365 number of days per year with phenophase activity
Biogeographical affinity	BA	1 = Ibero-Maghreb; 2 = Baetic; 3 = Sub-Mediterranean; 4 = Euro-Siberian
Winter bud type	WBT	1 = Scaled bud; 2 = Hypsophyllary bud; 3 = Naked bud

Table 3. Most representative phenological indexes in the studied species, measured as the number of months per year with phenophase activity: APS = active phenophasic period of the species; DVG = dolichoblast vegetative growth; FBF = flower bud formation; F = flowering; FS = fruit setting. RA = index of reproductive activity of the species (sum of number of months per year with reproductive phenophases as FBF, F and FS); RVA = index of reproductive/vegetative activity of the species (relationship between the sum of months with reproductive phenological phases as FBF, F and FS and the number of months with vegetative phenological phases as DVG); PSI = phenophase sequence index (degree of sequence of vegetative and reproductive phenophases); Max. F = month(s) of the annual cycle with the highest flowering percentage; t(FS) = period of time in months with the presence of fruiting phenophase (short 1 month -S-, medium 2-3 months -M-, long-lasting 4-5 months -L-, very long-lasting 6 or more months-VL-); t(SD) = period of time in months with presence of dispersal phenophase (short 1 month -S-, medium 2-3 months -A-, long-lasting 4-5 months -L-, very long-lasting 6 or more months-VL); Max.DVG = month of the annual cycle with the maximum DVG in cm; LA = period of time in months of the annual cycle with leaf activity phenophase; LS = period of time in months of the annual cycle with presence of leaf senescence phenophase; LAS = index of leaf activity/senescence of the species; PPT = phenophasic pattern (type I -growth simultaneous with flowering-, type II -flowering before growth- and type III -growth before flowering-). FGi = flowering and growth overlap index (months where flowering and growth overlap/ months where flowering and growth non-overlapping).

Indexes/species	APS	DVG	FBF	F	FS	RA	RVA	PSI	Max. F	t(FS)	t(SD)	Max.DVG	LA	LS	LAS	PPT	FGi
Acer granatense	8	2	2	1	7	10	5.00	0.60	V	7, VL	2,M	V 9.5	7	2	3.50	I	1
Berberis hispanica	6	3	3	1	4	8	2.67	0.57	VI	4, L	2, M	VII, 20	6	4	1.50	III	1
Betula fontqueri	12	5	10	2	6	18	3.60	0.71	V	6, VL	3, M	VII, 80	6	2	3.00	III	0.66
Cotoneaster granatense	9	5	2	1	5	8	1.60	0.63	VI	5, L	1, S	V, 8	8	2	4.00	III	0.25
Crataegus granatense	7	4	2	1	6	9	2.25	0.57	V	6, VL	4, L	VI, 10	7	2	3.50	III	0.33
Fraxinus excelsior	10	6	2	3	6	11	1.83	0.36	III–IV	6 ,VL	3,M	V 15	6	3	2.00	III	1
Lonicera arborea	7	2	2	2	5	9	4.50	0.50	V	5, L	2,M	V, 14.5	8	2	4.00	III	0.5
Malus sylvestris	6	3	2	1	4	7	2.33	0.50	V	4, L	4, L	VI 5	7	4	1.75	III	0.5
Prunus avium	5	3	2	2	3	7	2.33	0.57	IV	3, A	1, S	V 13.5	7	4	1.75	I	2
Prunus ramburii	7	5	2	1	6	9	1.80	0.63	V	4, L	5, L	VI, 41	7	3	2.33	III	0.25
Quercus pyrenaica	7	2	1	2	5	8	4.00	0.50	V	5, L	2,M	VI 7.5	7	4	1.75	I	∞
Quercus x trabutii	7	3	1	1	6	8	2.67	0.50	V	6, VL	2,M	VI 10	8	3	2,67	III	0.5
Rhamnus cathartica	6	2	2	1	4	7	3.50	0.60	V	4, L	1, S	V, 8	8	4	2.00	I	1
Rosa corymbifera	7	3	1	1	5	7	2.33	0.60	VI	5, L	2,M	V 14.5	7	4	1.75	III	0.5
Salix caprea	6	2	4	2	3	9	4.50	0.63	IV	3, A	2, M	VI, 2	7	2	2.50	II	0.5
Sorbus aria	6	2	2	1	5	8	4.00	0.40	VI	5, L	3, M	VI, 10	6	2	3.00	III	1
Sorbus hybrida	7	2	2	1	5	8	4.00	0.60	V	5, L	2, M	VI, 5	6	1	6.00	I	1
Taxus baccata	8	2	2	1	6	9	4.50	0.60	V	6, VL	5, L	VI, 4.5	12	3	4.00	I	1

phenophases. The difference between FGi and PPT is that the latter index includes the pre-flowering (FBF) in the reproductive phenophases and FGi only includes flowering (F).

Other new indexes

- Max. F: month(s) of the annual cycle with the highest flowering percentage.
- t(FS): period in months with the presence of fruiting phenophase (short: 1 month -S-, medium: 2–3 months -A-, long-lasting: 4–5 months -L-, very long-lasting: 6 or more months -VL-).
- t(SD): period in months with presence of dispersal phenophase (short: 1 month -S-, medium: 2–3 months -A-, long-lasting: 4–5 months -L-, very long-lasting: 6 or more months -VL-)
- Max. DVG: month of the annual cycle with the maximum DVG in cm, measured in the longest branches.

Day of initiation of phenophases

Following Denny et al. (2014, 2023) for the phenophases of flowering (F), leaf activity (LA) and senescence (LS), the day of initiation in the annual cycle was calculated for each species studied (i.e. the number of the day of the year among 0–365 when the phenophase activity begins); day of initiation of flowering (DiF); day of initiation of leaf activity (DiLA); and day of initiation of leaf senescence (DiLS).

Counting of phenophasic days

To determine the period in which all the studied phenophases were active, the time scale was transformed from months to days of the year (i.e. from day 1 to day 365 of the study year). Each phenophase present a duration in days of year (Denny et al. 2014, 2023) that was calculated as the difference between the phenophase start day and the end day in the study year.

Annual sequence of the phenophases of the community and phenological functional groups

The reproductive and vegetative phenophases at a community level were displayed as line graphs showing the monthly percentage of species reached for each phenophase.

The APC index or 'active phenophasic period of the plant community' was calculated following Pérez-Latorre and Cabezudo (2002).

For the identification of functional groups (FG) (Zanzottera et al. 2020), we used the 15 phenophasic stages and two measurable variables related to phenomorphology and climate:winter bud type (WBT) and biogeographical affinity (BA). WBT was studied according to Nitta and Oshawa (1998) and was classified into three types from less-protected to much-protected buds: 1) naked buds, 2) hypsophilous buds (buds covered with a small number of immature or hypsophilic leaves), and 3) scaled buds. BA was selected according to Blanca et al. (2011) and GBIF 2023 (the global biodiversity information facility) database, using the following categories which expressing a transition from dry thermic areas to wet cold areas: 1 = Ibero-Maghreb; 2 = Baetic; 3 = Sub-Mediterranean; 4 = Euro-Siberian.

Following Pérez-Latorre and Cabezudo (2002, 2006) and Hidalgo-Triana et al. (2023), we calculated the strategies richness index (SRi), which is defined as the ratio between the number of functional groups (FG) and the total number of species in the community. Low values indicate a poor representation of different FGand functional homogeneity and high values richness in FG and a possible refuge of relict taxa.

Statistical analysis

To classify the species based on selected phenological phases and indices, a data matrix of number of days per year with phenophase activity was constructed (Supporting information) to determine phenological similarity (cluster analysis) and identify the axes of greatest variation in the phenophases (PCA) of the species and variables studied (Table 2). Only the variables with the greatest variance in the number of days per year with phenophase activity have been applied:fruit growth (FSg); seed dispersal (SD); young leaves (LAy) and adult green leaves (LAag). Both analyses were developed with the PAST software ver. 4.09 (Hammer and Harper 2022).

The presence–absence data collected on the field sheets for the phenophases (events) of each of the species studied were taken to phenological event monitoring plots (Denny et al. 2014, Denny and Crimmins 2023) from which the estimated start and end date of a given phenophase, the number of days per year with phenophase activity and the intensity of the phenological event in percent were obtained (e.g. flowering of *Prunus avium,* Supporting information). A cluster analysis and spatial biplot diagram based on the phenophases or sub-phenophases were made to establish functional groups (FG) following De Bello et al. (2011). The cut-off level of the clusters was chosen so the resulting functional groups (FG) were interpretable and in agreement with observations in the natural environment. Prior to the analysis, the variables were typified by dividing the mean by the standard deviation to avoid an unbalanced variable contribution.

Results

Annual phenophasic sequences of the species

Flower bud formation (FBF) in most species (15) was concentrated in spring, except for *Fraxinus excelsior* and *Salix caprea* which occurred in winter, and for *Betula fontqueri*, which lasts almost the entire annual cycle. All species flowered (F) in spring, and reached a peak of maximum flowering in May; only *Fraxinus excelsior* flowered earlier in late winter (Supporting information). Fruiting (FS) was observed between spring and summer, and even extended into autumn. Dispersal (SD) occurred in late summer and throughout most of autumn.

Dolichoblast and brachyblast vegetative growth (DVG, BVG) occurred in all the species between late winter and spring (Supporting information), except for *Fraxinus excelsior* which began in winter (Supporting information).

Leaf activity (LA) occurred from spring to early autumn, except for the evergreen *Taxus baccata*, active throughout the annual cycle although with registered LAy only in May and June (Supporting information).

Senescence (LS) appears mostly (in 50–90% of species) between September and November (Supporting information). However, five taxa show early senescence in late summer (August), and *Lonicera arborea* in July and *Taxus baccata* between June and August (Supporting information).

Fallen leaves on the ground (FLG) has been observed in deciduous species in late autumn and early winter, except for the only evergreen species *Taxus baccata* presents this phenophase in the summer (Supporting information).

Species phenological patterns and indexes

Phenological indexes are available in Table 3.

The most frequent APS (active phenophase period of the species) values are medium (6–8 months) with 14 species, representing almost 78% of the activity. The lowest values (less than 6 months) were only found in *Prunus avium*, while the highest values (9–12 months) were achieved by three species, *Cotoneaster granatense* (9), *Fraxinus excelsior* (10) and *Betula fontqueri* (12) (Table 3).

All the species showed RVA (reproductive/vegetative activity of species) > 1, meaning a longer duration of reproductive phenophases over vegetative phenophases (Table 3).

PSI (phenophase sequence index) values ranged between 0.4–0.71. Half of the species showed phenophase overlap strategy (PSI < 0.6), such as *Fraxinus excelsior, Prunus avium, Malus sylvestris, Quercus x trabutii, Q. pyrenaica, Lonicera arborea, Crataegus granatense, Sorbus aria* and *Berberis hispanica* (50%).The other half showed a phenophase sequencing strategy (PSI ≥ 0.6), such as *Rosa corymbifera, Acer granatense, Cotoneaster granatense, Prunus ramburii, Rhamnus cathartica, Betula fontqueri, Taxus baccata, Sorbus hybrida* and *Salix caprea* (Table 3). Type III (first, growth; second, flowering with overlapping or not overlapping with growth) of PPT (species phenophase pattern) predominated in 11 species (61%), showing predominantly one month of overlapping. The type I (first, overlap in the first month; second, no overlap either of the two phenophases) pattern was found in 6 species (33.3%) and with the predominant initial subtype, as well as FGi = 1. The type II (first, flowering; second, growth with overlapping or not overlapping with flowering) pattern only occurred in *Salix caprea* (5.5%), the subtype is partial, and the FGi is 0.5 (Table 3, Supporting information).

LGI (Phenophase index of fallen leaves on the ground). Low values of LGI ≤ 3 were present in most of the studied species 14 (83%, deciduous species) but only three species had high values LGI ≥ 4 (17%, marcescent species), (Supporting information).

LAS (leaf activity/senescence index of the species). High values of LAS ≥ 4 were detectedin four taxa (22.2%); *Lonicera arborea, Cotoneaster granatense, Taxus baccata*, and *Sorbus hybrida*. Medium values (2 < LAS < 4) are present in seven taxa (38.8%) as *Quercus x trabutii, Acer granatense, Crataegus granatense, Prunus ramburii, Betula fontqueri, Sorbus aria* and *Salix caprea*. Low values (LAS ≤ 2) were shown by seven taxa (38.8%) as *Fraxinus excelsior, Prunus avium, Malus sylvestris, Rosa corymbifera, Quercus pyrenaica, Rhamnus cathartica* and *Berberis hispanica* (Table 3).

FGi (Flowering and growth overlap index). Values close to one FGi (high phenophase overlap) occurred in a total of seven species (39%), values close to zero FGi (phenophase sequencing) occurred in three species (17%). Intermediate situations occurred in eight species (44%) (Table 3).

Day of initiation of phenophases

Species with DiF < 88 are more than 60% of the species studied (Table 4); species with DiF around day 88 represents slightly less than 40% of the taxa; none of the studied species show DiF > 88 (Table 4).

Species with DiLA < 88 are represented by four deciduous tree species (slightly more than 20%), while the rest of the species (about 80%) show DiLA > 88 (Table 4).

Senescence peaks around day 273 of the annual cycle in mid-October. Species with DiLS < 273 are more than 80%. Two species would be around day 273 (slightly more than 10%; *Quercus pyrenaica* and *Cotoneaster granatense*). Only one species (slightly more than 5%) has DiLS > 273 (*Quercus x trabutii*) (Table 4).

Annual sequence of the reproductive phenophases of the community

Flower bud formation (FBF) occurred in spring, with an almost absolute maximum in May (more than 80% of species) although there is a relative maximum in April, with 70–80%. The minimum occurs between July and January, with 10% or less (Supporting information).

Table 4. Day of starting of the phenophasesin the annual cycle in each species of the deciduous forest community: flowering (DiF), leaf activity (DiLA) and senescence (DiLS).

Taxa	DiF	DiLA	DiLS
Acer granatense	58	58	239
Berberis hispanica	88	121	239
Betula fontqueri	58	88	239
Cotoneaster granatense	58	149	273
Crataegus granatense	58	88	239
Fraxinus excelsior	88	18	239
Lonicera arborea	58	88	239
Malus sylvestris	58	88	239
Prunus avium	58	58	239
Prunus ramburii	58	88	181
Quercus pyrenaica	88	88	273
Quercus x trabutii	58	88	301
Rhamnuscathartica	58	88	181
Rosa corymbifera	58	121	181
Salix caprea	88	58	239
Sorbus aria	88	121	239
Sorbus hybrida	88	88	273
Taxus baccata	88	88	121

Flowering (F) occurs in spring (May and June) with nearly 70% of the species. The minimum occurs between July and March, with less than 20% and April slightly reaching this percentage, due to the early flowering of *Prunus avium*, *Acer granatense* and *Salix caprea* (Supporting information).

Maximum fruiting (FS) occurs in July for100% of the species. In June, August and September it reaches 90% and then it starts to decrease although with values of up to 70% in October. The absolute minimum (0%) occurs mostly in winter (December–March) (Supporting information).

Dispersal (SD) occurs at the end of summer and throughout autumn (August–December). Maximum dispersion peak occurs in October with more than 80%and then sharply decreasing during autumn and becoming zero in winter. The dispersion minimum occurs between January and July (Supporting information).

Annual sequence of the vegetative phenophases of the community

Vegetative growth (DVG and BVG) was continuous from March to November (i.e. spring, summer and autumn), reaching 100% between June and October (summer and early autumn). Minimum growth is reached in winter (December–February) with less than 20% of species (Supporting information).

Leaf formation (LF) is at its peak from June to October (100% of the species) and minimum from December to March (5%). Leaf senescence (LS) reaches the maximum in autumn (October and November, 80–90%) and minimum from December to May (0%) (Supporting information). The maximum fallen leaves on the ground (FLG) is autumnal and wintry (November–December, 80–90%) and with a spring-like minimum from February to May (0%) (Supporting information).

Active phenophasic period of the community (APC)

The deciduous forest was highly active in spring (April–June), showing values of at least 70%, coinciding with the FBF showing approximately 80% of the species with flower buds. The absolute maximum (100%) occurs in May, coinciding with almost 70% of the species flowering (Supporting information). Medium APC values appear between late winter and early autumn (March–October), with values slightly above 30%. The minimum values are achieved in winter (December, January and February), reaching 0% in December and in January with 5% (Supporting information).

Phenological functional groups

The PCA showed that the two axes supported 64.9% of the variance. Component 1 is interpreted as reflecting a durability gradient in the vegetative growth subphenophase of stable buds formed (DVGfsb) that increases towards the positive direction of the x-axis, where the species with increased dispersion (SD) durability are located. In the opposite way, agradient in the sub-phenophase young leaf formation (LAy) was detected, where the species with the highest durability (LF) were located, can also be interpreted, albeit in a negative direction (Supporting information).The positive direction of component 2 is interpreted as a seed dispersal gradient; the species located in that area of the graph would show greater dispersal periods *Sorbus aria* and *Taxus baccata* (Supporting information).

In the deciduous forest, the clustering analysis (Supporting information) identified a large group of 15 taxa (correlation coefficient 0.93) (FG 4, Table 5) formed by 15 species from seven different families (*Rosaceae* with 8 taxa; *Fagaceae* with 2 and with 1 stand *Aceraceae*, *Caprifoliaceae*, *Rhamnaceae*, *Betulaceae* and *Berberidaceae*) with similar phenological functionality, although the analysis also sub-grouped three taxa sharply differentiated about phenological functionality (i.e. *Fraxinus, Taxus* and *Salix*) taking the Euclidean distance of 250. The biogeographic affinity and type of overwintering buds of each taxon had no significant impact on the cluster analysis (Supporting information).

The obtained SRi was 4/18 (i.e. 0.22). The fact of having used only phenological attributes must be considered to examine this result, as Sri has traditionally been used as for morphological functional characters only.

Discussion

Annual phenophasic sequences of the species

Only three of the 18 studied species demonstrated active-phenophases throughout the annual cycle: *F. excelsior*, *T. baccata* and *B. fontqueri*; these can beidentifiedascryo-active species, because they show phenophasic activity in at least one of the winter months (Kollas et al. 2014). *Fraxinus excelsior* shows FBF and DVG in mid-winter (Rosique-Esplugas et al. 2022) perhaps because this tree takes refuge in sheltered valleys (Tsai et al. 2016) and in less cold and protectedfrom windareas that do not typically exceed an altitude of 1400 m.

FBF and Fmostly occur in springwhich coincides with the main period recorded for Mediterranean flora. FS extends into autumn in most of the species due to the predominance of fleshy fruits with long maturation periods and so with dispersal in autumn as also occurs in tree and shrub species of Mediterranean forests. Growth was primarily recorded in spring and this is animportant difference with Mediterranean species, which can begin in autumn and winter (Pérez-Latorre and Cabezudo 2002, 2006, Milla et al. 2010, Recio and Silva-Marín 2018). Regarding the leaf activity (LA), it occurred in the annual climatic optimum (i.e. from spring to early autumn), when frost is unlikely. Autumn–winter senescence and FL separates nearly all of the studied species (except for *Taxus baccata* as an evergreen) from those of the Mediterranean forests and shrublands.

Table 5. FGs obtained for the winter deciduous forest plant community from cluster analysis. Only the variables with the highest variance have been included in this table. FSg: fruit growth (i.e. number of days per year with phenophase activity); SD: seed dispersal (i.e. number of days per year with phenophase activity); LAy: young leaves (i.e. number of days per year with phenophase activity); LAag: adult green leaves (i.e. number of days per year with phenophase activity).

Scientific name/ Functional traits	Fructification (fruit growth)	Seed dispersal (number of fruits per square meter)	Leaf formation (% of young leaves)	Leaf formation (adult green leaves)	Functional groups
	FSg	SD	LAy	LAag	
F. excelsior	93	152	304	213	**FG1:**Deciduous mesophanerophyte with high LF_1 and LF_2 and high SD (early and prolonged foliation and dispersal).
S. caprea	0	0	61	241	**FG2:**Deciduous mesophanerophyte with high LF_2 and very short FS_1 and SD (very short dispersal and fructification).
T. baccata	208	148	93	365	**FG3:**Evergreen mesophanerophyte with very high LF_2 and high FS_1 (very long-lasting foliation and fruiting).
P. avium	61	63	123	213	**FG4:**Deciduous mesophanerophytes,microphanerophytes and nanophanerophytes of high LF2 (long foliation).
M. sylvestris	60	148	72	213	
R. corymbifera	91	126	91	213	
Q. x trabutii	152	90	91	241	
Q. pyrenaica	124	90	61	208	
A. granatense	93	126	63	213	
L. arborea	91	90	63	241	
C. granatense	91	0	91	241	
Cr. granatense	91	148	63	213	
P. ramburii	124	148	63	213	
R. cathartica	60	62	93	180	
B. fontqueri	124	130	91	213	
S. aria	118	193	93	152	
S. hybrida	0	130	61	180	
B. hispanica	91	120	93	152	

Species phenological patterns and indexes

The detected presence of a dominant group (78% of species) with active phenophasic period of the species (APS) concentrated between the 6–8 warmest months indicates that the studied plants exhibit low phenophasic activity in the winter (Pérez-Latorre and Cabezudo 2002, 2006, 2012) and are well adapted to the hard-environmental conditions of the medium-high mountains, where *Betula fontqueri* stand out as the better adapted by showing activity throughout the year.

The detected predominance of the duration of reproductive over vegetative phenophases (RVA > 1) is common among phanerophytes (i.e. trees, both deciduous and evergreen), as Krishna and Garkoti (2022) found in the forests in Central Himalaya, and absolute opposite to chamaephytic shrublands (Pérez-Latorre and Cabezudo 2002, Hidalgo-Triana and Pérez-Latorre 2018).

The group of deciduous species with PSI < 0.6 would showa better adaptation to more thermal, foggy and mesic environments (Pérez-Latorre and Cabezudo 2002, 2006, 2012), responding with an overlapping of the phenophases. On the other hand, the group with PSI ≥ 0.6, where phenophase sequencing predominates, would be a group with adaptation to colder and continental environments (Souto-Herrero et al. 2005, Civantos et al. 2020).

A majority of our studied species (more than 60%) showed an asynchronous PPT type III, which possibly responds to environmental conditions that imply a sequencing of phenophases in a favourable period for deciduous trees in their annual cycle of no more than 6–8 months (spring plus summer). Branch architecture may also have to deal with type III, as some species must wait the elongation of vegetative branches to form flower buds (Castro-Díez and Monserrat-Martí 1998, Pérez-Latorre and Cabezudo 2012). The predominance of the type III asynchronous (>60%) in the winter deciduous forest followed by type I synchronous (>33%) is opposite to which was detected by Pérez-Latorre et al. (2007) in evergreen forests, with a predominance of type I (56%), followed by type III with 44%. The concurrence of phenophases in time requires a significant number of resources in a short period of time (mainly spring) (Mooney 1983), perhaps justified by a subsequent period of stress after spring in the genuine Mediterranean climate (Sánchez de Dios et al. 2009). On the contrary, the sequencing of phenophases (i.e.

growth before flowering) allows for better management in time of resources that can even be directly generated from already formed leaves (Mooney and Kummerow 1981); this case of sequencing may also depend on ontogenetic growth of organs of the plant, because flowers may be formed a -posteriori from previous growing branches, and so, the pattern may be controlled genetically as in some conifers (i.e. *Abies*, Pérez-Latorre and Cabezudo 2012) and making PPT independent from taxonomic families (Table 3).

Deciduous taxa with low LAS and LGI indices (e.g. *Fraxinus*) would complete their functional cycle more efficiently in warm seasons such as spring and summer (Bayura et al. 2018, Rosique-Esplugas et al. 2022) which would indicate a better adaptability to sub-Mediterranean environments in Mediterranean areas (Civantos et al. 2020) on the contrary taxa with high LAS and LGI values, probably more heliophilous (e.g. *Lonicera*) would present lower functional efficiency and possibly worse adaptability to a changing climate.

Regarding FGi index, it did not show a clear predominance between sequencing and overlapping flowering and growth of the species studied. This is possibly due to the mixed-forest character and diverse taxonomic origin of this plant ecosystem rather than to environmental conditions. The overlapping of DVG and F could be interpreted, however, as a better adaptation to the sub-Mediterranean climate than sequencing (Pérez-Latorre and Cabezudo 2012) (i.e. less dry, colder) and rather than an adaptation to the typical warm, dry Mediterranean climate (Milla et al. 2010).

Day of initiation of phenophases

The day of flowering initiation (DiF) (Denny et al. 2014) observed in species with DiF < 88 (60%) (e.g. *Acer granatense*, *Betula fontqueri* or *Prunus avium*) were considered early flowering, because maximum flowering in mid-April, which approximately corresponds to day 88 of the annual cycle. Species identified with DiF around day 88 (40%) (would have a standard or normal flowering) while DiF > 88 were considered late flowering but have not been detected.. An index DiLA < 88 observed before mid-April has been identified as early-leaf activity for 20% of species (e.g. *Fraxinus excelsior* or *Salix caprea*), the rest of studied species (about 80%) would be classified as standard or normal leaf activity. Species identified with DiLS < 273 (80%) would be considered early in this phenophase. Two species were detected around day 273 (*Quercus pyrenaica* and *Cotoneaster granatense*) with standard senescence. Only one species obtained DiLS > 273 *Quercus x trabutii* and was considered late in this phenophase.

Annual sequence of the reproductive phenophases of the community

May, with more than 80% of species exhibiting flower buds is considered the peak season for this phenophase in the studied ecosytems, unlike in Mediterranean ecosystems (*Quercus suber* forests), which experience pre-flowering in late spring and early summer, or even in winter (Pérez-Latorre and Cabezudo 2002, Hidalgo-Triana and Pérez-Latorre 2018, Hidalgo-Triana and Pérez-Latorre 2021). Among the studied species, a functional differentiation can be observed in relation to flower buds, which makes it possible for such species as *Fraxinus excelsior*, *Prunus ramburii* or *Salix caprea* to flower early, even before leaf unfolding because they form stable flower buds on old branches (Pérez-Latorre and Cabezudo 2012). Other species need new branches to be formed first (DVG) to develop flower buds and then flowers, as is the case, for example, with *Quercus pyrenaica* or *Q. x trabutii.*

Flowering in summer and autumn is practically nil, unlike in Mediterranean evergreen forests ecosystems, which, even though they mainly flower in spring (Navarro and Cabezudo 1998, Pérez-Latorre and Cabezudo 2002, Pérez-Latorre et al. 2007, 2009) and depending on the mildness of the climate, may show secondary flowering peaks in other seasons, such as autumn or even winter. Compared to other typically Mediterranean communities with more extensive flowering, there stricted flowering seasonality in just two or three months of spring could highlight the biogeographical Euro–Siberian origin of the phenological functionality of the studied plant community (Tal 2011).

The particularity of having the maximum peak of fruiting (F) in summer (July) could resemble this ecosystem with the northern deciduous forests (*Querco–Fagetea* class) as well as with other Mediterranean mesophyll forests (*Quercetalia ilicis* order), where the reproductive phenological phases (i.e. fruiting and seed dispersal) are longer and later due to the predominance of fleshy fruits and zoochory, as opposed to the typical Mediterranean scrub (*Rosmarinetea*, *Cisto–Lavanduletea* classes) with dry fruits and mechanical seed dispersal (Pérez-Latorre and Cabezudo 2002).

Regarding SD, we detected a coincidence with typical Mediterranean plant ecosystems due to the occasional concurrence with the type of fruit predominantly fleshy and, in other cases, the mode of dispersal (Pérez-Latorre and Cabezudo 2002, Hidalgo-Triana and Pérez-Latorre 2018, 2021).

Reproductive phenophases experience peaks concentrated between May and October, taking advantage of the time of year with a favourable climate, frost-free with wet soil (Blanco et al. 1997, Montgomery et al. 2020). On the contrary, in the *Quercus* mediterranean forest, these same phenophases have peaks that are sequenced throughout the annual cycle due to the mild climate where they live, giving rise to a time lag of approximately one month between both ecosystems (Pérez-Latorre and Cabezudo 2002).

Annual sequence of the vegetative phenophases of the community

Vegetative growth was continuous in spring, summer and autumn because environmental conditions (temperature and rainfall/water presence in the soil) were favourable. However, minimum growth (both DVG and BVG) is reached in winter, when mean monthly temperatures remain below 7°C and frosts are frequent (Rivas-Martinez 2007). Both winter deciduous forest and evergreen *Quercus* forests (Pérez-Latorre and Cabezudo 2002) show maximum growth during spring. The maximum of BVG and DVG in evergreen forests occurs simultaneously in May, while in our studied forest, the BVG peak is earlier (February–May) than the DVG (May–June).

Leaf activity (LA) marks the more favourable climatic period in the annual phenological cycle (Blanco et al. 1997, Blanca 2000), and generally occurs from early spring to mid-autumn (April–October). Currently, the deciduous forest is named as a 'summer forest' in the sense of full functioning when it shows its phenological and functional optimum (Rosique-Esplugas et al. 2022).

Leaf senescence (LS) and fallen leaves on the ground (FLG) are closely related phenophases which are active in autumn and early winter and mark the unfavourable conditions for functional seasonality. Maximum peak in LS is autumnal coinciding with declining in leaf-activity and shows minimum in December with presence in less than 10% of the species, which coincides with the maximum peak of FLG, and 90% of the species without leaves in their canopy (except for *Taxus*). In evergreen *Quercus* forests, leaf fall is partial and occurs throughout the entire annual cycle with the maximum in July and August due to summer drought (Navarro and Cabezudo 1998, Pérez-Latorre and Cabezudo 2002, Pérez-Latorre et al. 2007, Recio and Silva-Marín 2018).

Active phenophasic period of the community (APC)

The environmental conditions (temperature and rain/humidity) are optimal in the maximum APC (spring) and the number of active phenophases, both reproductive and vegetative, is therefore high. The minimum APC values correspond to the end of autumn and throughout the winter (December, January and February) which coincides with the most limiting climatic conditions, a typical situation in northern Euro–Siberian deciduous forests (Molero and Marfil 2017) but due to the existence of a weak sub-Mediterraneanin the study area that is a hidden Eurosiberian character contributes to the survival of this relict forests. Mediterranean evergreen forests reach maximum APC in May and June with 100% and maintains above or equal to 70% in all months of the annual cycle (Pérez-Latorre and Cabezudo 2002). It could be said that it is a phenologically active ecosystem throughout the annual cycle (multi-seasonal in the sense of Orshan 1989). In contrast, the deciduous forest has APC index values above 70% for only four months of the annual cycle-from April to June. It could be said that the deciduous forest is more stenoic, formed by species that have a narrow range for environmental factors, occupy less surface area and specific territories. at the functional level, contrary to the Mediterranean evergreen forest, which is more eurioic, formed by species that present a wide range of values for environmental factors, occupy a larger surface area and diverse territories (Blanco et al. 1998, Manzano et al. 2019).

Phenological functional groups

In this study, the statistical analysis detected four pheno-functional groups (Pérez-Harguindeguy et al. 2013) that practically coincide with the two PCAs mentioned in the previous section. Three groups are formed by a single species (monospecific phenogroup), indicating a high functional diversity. The case of *Fraxinus excelsior* (Tsai et al. 2016, Bayura et al. 2018, Rosique-Esplugas et al. 2022) stands out due to its early vegetative growth (DVG) in midwinter while in the case of *Salix caprea* it is due to its early onset of reproductive phenophases (FBF) (Choudhary et al. 2011) and for the gymnosperm *Taxus baccata* is due to its leaf senescence phenophase (Cunninghame et al. 1979) in mid-summer and prolonged sub-phenophase of fruit growth (FSg). As for some singular characteristics, *Fraxinus* has a riverside and warm habitats affinity in northern mixed forest (Tsai et al. 2016), *Salix* reaches high altitudes in Sierra Nevada with very cold climate and accompanying *Betula* in unstable environments as first-colonisers and *Taxus* is a gymnosperm and evergreen.

On the other hand, the most numerous phenogroup is made up of 15 species, although there may be stated subgroups of closely related species, as one constituted by *Prunus avium*, *Rhamnus cathartica*, *Rosa corymbifera*, *Quercus* x *trabutii*, *Q. pyrenaica*, *Lonicera arborea* and *Crataegus granatense*, a mix of forest trees and their mantle of tall shrubs. Compared to other studies in Mediterranean climate ecosystems (Navarro et al. 2010, Hidalgo-Triana and Pérez-Latorre 2018), a lower diversity of pheno-functional groups was obtained. The Sri of 0.22 was rather low, which indicates that habitat suitability is driving a pronounced adaptation to the environment and phenological functionalism in most of the species, also above taxonomic-phylogenetic or morphological considerations (Orshan 1986). Biogeographical origin and type of buds have no incidence in the identification of functional groups but may explain other functional traits not studied in this work (i.e. morphological traits) which may have changed the number of FG and thus the SRi index value.

Conclusions

The winter deciduous forest in the south of the Iberian Peninsula presented different phenophase patterns to the neighboring Mediterranean evergreen plant communities, mainly in terms of phenophasic pause and senescence in winter. Most of the species studied showed high phenological activity in late spring and summer and only remained mostly inactive during winter. In addition, they generally tend to invest more time and resources in reproductive functions to the detriment of vegetative functions and to show themselves as non-sequencers due to the continentality climate with very cold and freezing winters. The species studied tend to a greater or lesser degree to overlap their phenophases, concentrating on the mild seasons, spring and summer where functionality reaches its peak. A predominance of asynchronicity was observed with sequencing in growth, flower bud formation and flowering with or without overlap.

Winter deciduous forests in the southern latitudes of the European continent represent a phenological and functional uniqueness of great ecological value, they are currently threatened and deserve priority conservation.

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Author contributions

Manuel Pavón-Núñez: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Writing – original draft (equal). **Noelia Hidalgo-Triana**: Conceptualization (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Andrés V. Pérez-Latorre**: Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1zcrjdg47 (Pavón-Núñez et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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