

## RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

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# Forest resilience to global warming is strongly modulated by local-scale topographic, microclimatic and biotic conditions

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**Abstract**

1. Resilience of endangered rear edge populations of cold-adapted forests in the Mediterranean basin is increasingly altered by extreme heatwave and drought pressures. It remains unknown, however, whether microclimatic variation in these isolated forests could ultimately result in large intra-population variability in the demographic responses, allowing the coexistence of contrasting declining and resilient trends across small topographic gradients. Multiple key drivers promoting spatial variability in the resilience of rear edge forests remain largely unassessed, including amplified and buffered thermal exposure induced by heatwaves along topographic gradients, and increased herbivory pressure on tree saplings in defaunated areas lacking efficient apex predators. Here we analysed whether indicators of forest resilience to global warming are strongly modulated by local-scale topographic, microclimatic and biotic conditions.
2. We studied a protected rear edge forest of sessile oak *Quercus petraea*, applying a suite of 20 indicators of resilience of tree secondary growth, including multidecadal and short-term indices. We also analysed sapling recruitment success, recruit/adult ratios and sapling thermal exposure across topographic gradients. We found large within population variation in secondary growth resilience, in recruitment success and in thermal exposure of tree saplings to heatwaves, and this variability was spatially structured along small-scale topographical gradients. Multidecadal resilience indices and curves provide useful descriptors of forest vulnerability to climate warming, complementing assessments based in the analysis of short-term resilience indicators. Species-specific associations of trees with microclimatic variability are reported.
3. Biotic factors are key in determining long-term resilience in climatically stressed rear edge forests, with strong limitation of sapling recruitment by increased roe

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deer and wild boar herbivory. Our results also support non-stationary effects of climate determining forest growth responses and resilience, showing increased negative effects of warming and drought over the last decades in declining stands.

4. *Synthesis.* Our findings do not support scenarios predicting spatially homogeneous distributional shifts and limited resilience in rear edge populations, and are more supportive of scenarios including spatially heterogeneous responses, characterised with contrasting intra-population trends of forest resilience. We conclude that forest resilience responses to climate warming are strongly modulated by local-scale microclimatic, topographic and biotic factors. Accurate predictions of forest responses to changes in climate would therefore largely benefit from the integration of local-scale abiotic and biotic factors.

#### KEYWORDS

defaunation, drought, forest resilience, global warming, heatwave, land-atmospheric feedbacks, mammal herbivory, microclimate

## 1 | INTRODUCTION

Rear edge tree populations of cold-adapted temperate species are especially vulnerable to global change in the Mediterranean basin (Hampe & Petit, 2005; Pulido et al., 2019; Vilà-Cabrera & Jump, 2019). In Mediterranean rear edge forests, one of the most threatening components of global change is the increased frequency, intensity and duration of droughts and summer heatwaves (Carnicer, Domingo-Marimon, et al., 2019; Jump & Peñuelas, 2006; Spinoni et al., 2019; Turco et al., 2017; Vicente-Serrano et al., 2014). Despite increasing climatic impacts, recent studies report limited demographic declines and retraction in the distribution of many temperate trees in the Mediterranean basin, suggesting sustained demographic resilience to current climatic impacts (Batllori et al., 2020; Dittmar et al., 2003; Granda et al., 2018; Hackett-Pain & Friend, 2017; Tegel et al., 2014; Vilà-Cabrera et al., 2019). However, the mechanisms enhancing forest resilience in spite of increased warming impacts in rear edge areas still remain poorly understood for most dominant tree species (Canadell & Jackson, 2021; Granda et al., 2014; Lloret & Batllori, 2021; Lloret et al., 2012; Muffler et al., 2020; Vilà-Cabrera & Jump, 2019). Altitudinal and topographic gradients in rear edge areas can determine locally heterogeneous demographic responses to increased warming (Granda et al., 2018; Hackett-Pain & Friend, 2017). However, the modulation by local-scale topographic gradients of the impacts of extreme summer heatwaves in relict forests remains poorly quantified. Similarly, studies assessing the negative synergistic effects of the multiple drivers of global change in the resilience of rear edge forests are also warranted. For example, we lack detailed studies jointly considering in rear edge areas the coupled effects of increased drought, extreme summer heatwave events and altered networks of mammal herbivores negatively affecting tree sapling recruitment (Cairns & Moen, 2004; Castro et al., 1999, 2004; Den Ouden et al., 2005; Munier et al., 2010).

Imbalanced networks of mammal herbivores stand as a potentially important, but currently unassessed, driver of reduced demographic resilience in forest rear edge areas in the Mediterranean basin (Cairns & Moen, 2004; Gómez & Hódar, 2008; Munier et al., 2010). Human-induced global defaunation processes can alter local interaction networks and introduce drastic changes in the processes determining forest demographic resilience (Estes et al., 2011; Young et al., 2016). Studies in multiple land ecosystems indicate that the defaunation of top predators can facilitate an overabundance of large herbivorous mammals and drastically change forest dynamics (Estes et al., 2011; Gómez & Hódar, 2008; McLaren & Peterson, 1994; Nogués-Bravo et al., 2016; Ripple & Beschta, 2007; Roemer et al., 2009; Smit et al., 2015). For example, in the eastern Iberian Peninsula the historical defaunation of apex predators (wolves) has facilitated over the last decades the expansion of consumers of tree saplings and tree roots such as the Roe deer *Capreolus capreolus* and the wild boar *Sus scrofa* (Giménez-Anaya et al., 2020), increasing pressure on tree saplings at the regional scale. Tree sapling recruitment is a key process determining demographic resilience in rear edge areas of Mediterranean forests (Carnicer et al., 2014; Granda et al., 2014). This process could be largely impaired by increased herbivory in areas affected by long-term processes of defaunation of top predators and reduced human hunting pressure on large mammal herbivores (Côté et al., 2004; Mayer et al., 2000; Partl et al., 2002). In Mediterranean rear edge areas large population expansions of wild boar and roe deer are currently co-occurring, potentially affecting key rear edge areas (Barrios-García & Ballari, 2012; Giménez-Anaya et al., 2020; Massei & Genov, 2004; Saez-Royuela & Tellería, 1986). Management efforts to control increasing populations of wild boar and roe deer often obtain limited results, due to multiple logistic limitations and social barriers impeding an optimal human hunting pressure (Giménez-Anaya et al., 2020; González-Crespo et al., 2018; Massei et al., 2015; Vicente et al., 2019).

Beyond the effects of altered networks of mammal herbivores, other local-scale factors, such as local gradients of microclimatic and soil conditions can importantly determine the vulnerability of rear edge forests to global change (Graae et al., 2018; Granda et al., 2014; Herrera & Bazaga, 2008; Lenoir et al., 2017; Vilà-Cabrera et al., 2019; Zellweger et al., 2020). Topographical features (e.g. the steepness and aspect of slopes, elevation) and canopy cover can largely modify local heat exchanges at fine scales, altering climatic exposure of saplings and adult trees and potentially increasing forest resilience to climatic extremes (Bramer et al., 2018; Carnicer, Stefanescu, et al., 2019; Carnicer et al., 2017; Körner & Paulsen, 2004; Scherrer & Körner, 2010). Previous studies highlight that heterogeneity of microclimatic conditions at these scales can be especially relevant for seedling establishment and tree recruitment (Dobrowski et al., 2015; Lloret et al., 2005; Príncipe et al., 2019; von Arx et al., 2013).

To effectively assess demographic resilience in forest rear edge areas under pressure, detailed integrated measurements of microclimatic buffering effects, exposure of saplings to summer heatwaves and mammal sapling predation are needed. To address this knowledge gap, here we aim to evaluate the demographic resilience of a rear edge population of sessile oak (*Quercus petraea* Liebl.), assessing tree growth, recruitment rates and herbivore damage patterns along a topographic gradient in a protected Mediterranean mountain range. For this, we will address the following specific objectives: (a) to measure microclimatic exposure in oak tree saplings during an extreme summer heatwave event attributed to climate change (van Oldenborgh et al., 2019), assessing the operation of local buffering effects of the topographic gradient on the observed thermal exposure, (b) to describe the variability of tree sapling recruitment and herbivore damage along the topographic gradient, (c) to analyse the contrasting patterns of tree secondary growth and resilience between climatically exposed and buffered areas of the topographic gradient.

## 2 | MATERIALS AND METHODS

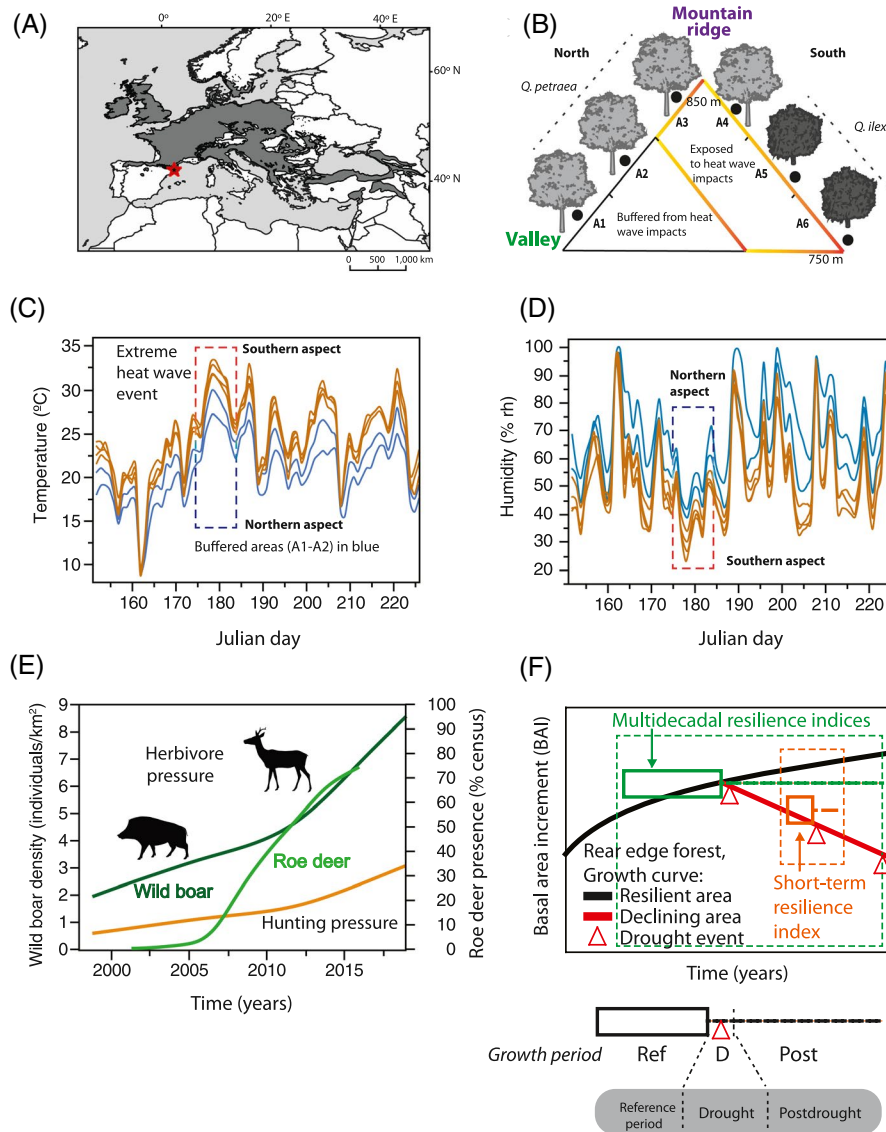
### 2.1 | Study area

More than 25 *Quercus* species inhabit the Mediterranean basin (Castagneri et al., 2020), including relict populations of deciduous oak species such as the sessile oak (*Q. petraea*). This species shows a higher susceptibility to drought in comparative ecophysiological studies (Arend et al., 2011; Bréda & Granier, 1996; Corcuera et al., 2002; Shestakova et al., 2014). This study analyses demographic resilience in an isolated sessile oak population located at the southernmost limit of the species distribution in the Iberian Peninsula (Figure 1A). This forest stand is remarkable for its large extension (4 ha), maturity and conservation state, given that along rear edge Mediterranean areas well-developed stands of *Q. petraea* are rather uncommon due to intensive logging over the last century (Bou & Vilar, 2019). The studied population is located within the Natural Park of Sant Llorenç del Munt i l'Obac, in Catalonia (NE Iberian Peninsula), at 40 km

inland from the Mediterranean Sea. This protected area (13,694 ha) comprises mid-altitude mountain ranges (300–1104 m) covered by mixed Mediterranean oak and pine stands (*Quercus ilex*, *Quercus humilis*, *Quercus petraea*, *Pinus halepensis*, *Pinus nigra* and *Pinus sylvestris*). Forests are dominated by mature successional stages (with ages in dominant trees >100 years), with abundant and well-developed holm and sessile oaks and limited pine regeneration dynamics (Carnicer et al., 2014). The current forest structure is the result of a multidecadal period of rural abandonment since the 1950s and the lack of active forest management in most of the protected areas of the park. *Quercus petraea* stands are restricted to isolated mesic sites in north-facing hillsides, whereas the most xeric sites are covered by Mediterranean mixed stands of holm oak (*Q. ilex*), Aleppo pine (*P. halepensis*) and xeric shrublands. In the study area, sessile oak stands are distributed in a relatively narrow topographic band (750–890 m), dominating the northern side of the mountain range and completely surrounded by holm oak forests. Sessile oak stands are restricted to humid areas but sparse individuals also colonise and develop in the elevated areas of southern-facing slopes (Figure 1B). While *Q. ilex* was fairly abundant and present in all topographic areas sampled, sessile oak saplings and adults were absent or rarely observed in the warmer southern-oriented bands A5 and A6 (Figure 1B). In contrast to these Mediterranean isolated rear edge areas, sessile oak is a very abundant tree at higher latitudes of the European continent, growing preferentially in humid areas in both calcareous and siliceous soils (Figure 1A). Pine species in the sampled area were represented by a few isolated and very scarce adult individuals of *P. halepensis* (located in the south-facing slope areas, i.e. the topographic bands A4–A6 in Figure 1B). A few isolated individuals of *P. sylvestris* were also detected in elevated northern-facing areas (i.e. corresponding to the topographic band A3 in Figure 1B). Due to this marginal presence and representation in the studied forest stands, trends for pine species were subsequently not considered in the analyses of forest resilience.

#### 2.1.1 | Extreme summer heatwave event and quantification of microclimatic exposure in tree saplings

In late June 2019 south-western and central Europe experienced the hottest summer heatwave event recorded in the available instrumental records (Sousa et al., 2019; Zhao et al., 2020). The heatwave was related to a persistent atmospheric wave train propagating eastward from the mid-high latitudes of the North Atlantic to Eurasia (Zhao et al., 2020) and has been linked to climate change in the available attribution studies (van Oldenborgh et al., 2019). Record-breaking temperatures for the month of June were recorded at many locations in Europe, including France, Switzerland, Austria, Germany, the Czech Republic, Italy and Spain. For example, France experienced temperatures in excess of 45°C for the first time in recorded history (van Oldenborgh et al., 2019). Along the studied topographic gradient, we measured the modulation of thermal



**FIGURE 1** The study zone is a rear edge forest of *Quercus petraea*, which has been recently impacted by heatwave dynamics, and increasing mammal herbivore pressure dynamics. (A) The map illustrates the location of the isolated rear edge population of *Q. petraea* (star symbol), in relation to the continuous continental distribution of this species in western Europe. (B) A diagram of the sampling units defined along the topographic gradient in the rear edge population (topographic bands A1–A6). Three topographic bands were distributed between 750 and 850 m [A1–A6: 750–783 m (elevational range: 33 m); A2–A5: 784–817 m; A3–A4: 818–850 m]. Black dots indicate the location of temperature–humidity sensors allowing the measurement of microclimatic variability and tree sapling thermal exposure during an extreme summer heatwave (June 2019). As illustrated in the diagram, in the studied rear edge forest the drought-sensitive *Q. petraea* is restricted to northern slopes and high elevation areas (i.e. ridge areas, 850 m a.s.l.), being progressively replaced by *Quercus ilex* stands in south facing slopes (topographic bands A5 and A6 in panel B). (C) Observed temporal dynamics of midday understory temperatures at 25 cm height during the studied extreme summer heatwave period (coloured rectangle). (D) Observed temporal dynamics of air humidity (25 cm height) in the understory during the extreme summer heatwave event. (E) Temporal dynamics of wild boar and roe deer densities in the studied forest rear edge area, showing a sustained increase over the last decade. Roe deer densities are expressed in percentage of detection in field censuses (Rosell et al., 2019). The orange line depicts the hunting effort in the study area (hunted wild boar individuals/km<sup>2</sup>). (F) A diagram summarising the multidecadal and short-term resilience indices applied in the study of secondary growth [measured as Basal Area Increment (BAI) in declining (red line) and non-declining areas (black line) of the rear edge forest]

exposure in continuously monitored oak saplings in the peak of this unprecedented heatwave event. To assess how topographic variability, aspect and slope modified tree sapling thermal exposure and humidity conditions, the study zone was divided into six topographic

bands (A1–A6 in Figure 1B, 750–850 m). These topographic bands comprised the north and the southern slope of the studied rear edge forest (Figure 1B). To continuously assess the spatial variation in climatic exposure, six temperature–humidity sensors (EL-USB-2, Lascar

Electronics) were distributed in early spring across the mountain range (Figure 1B, black dots), covering the whole altitudinal range of the sessile oak stand. The automatic sensors were located at 25 cm height above the soil surface using metal stakes, and were protected from direct solar radiation by a plastic envelope sustained by a wire-mesh cylinder (installed 5 cm above the sensor and thus precluding the direct incidence of solar radiation), recording microclimate data with hourly frequency. To assess thermal exposure outside the forest stand, an additional LASCAR temperature–humidity sensor was installed in an open bare ground area in the southern slope of the range (800 m, in the middle of the topographic band A5, in a forest gap area). This additional LASCAR sensor was also installed at 25 cm height above the soil surface and protected from direct solar radiation. In addition, using portable thermocouples and thermo-hygrometer devices, we measured with monthly resolution in all topographic bands (A1–A6) spring and early summer midday soil humidity (11:00 a.m. to 16:00 p.m.), soil temperature (1–15 cm depth), soil surface temperature, tree sapling leaf temperatures and air temperature at 2.5, 5, 10, 25, 50 and 100 cm height. Six measurement points were established in each topographic band (A1–A6) and in the control forest gap area (A5–open area without canopy) and were visited in April, May and June. We used temperatures measured at 1 m height as a reference for calculating positive and negative thermal offset values at different height levels (see Table S1, De Frenne et al., 2021). Canopy cover (percentage) was visually estimated in all these sites in a zenithal area of 1 m<sup>2</sup> above the focal point of thermal measurement (see Carnicer, Stefanescu, et al., 2019; Vives-Inglá et al., 2020 for methodological details).

In the six sampling points established in each topographic band monthly soil humidity measurements were performed using *DELTA-T SM150* (Delta-T Devices Ltd), ambient humidity measures were taken with *Thermo-hygrometer DC108* (Bonajay Technology Ltd). A thermocouple *Hanna HI935005N* type K (Hanna Instruments Ltd) was also used for the measurement of leaf, soil surface and air temperatures. Soil underground temperature was measured employing *Hanna HI98509* (Hanna Instruments Ltd). In each topographic band (A1–A6), we randomly selected and marked three saplings of both holm and sessile oak for continuous monitoring of temperature and humidity conditions with monthly frequency using thermocouples. Saplings were <130 cm high, corresponding to the first and second sapling size categories of the Spanish National Forest Inventory (R1 and R2, Table S1, Coll et al., 2013). All saplings selected were identified with plastic labels and georeferenced. For all microclimatic thermal measurements, we calculated thermal warming and cooling effects relative to reference measurements (i.e. local air temperatures measured at 1 m height without direct radiation incidence, see Carnicer et al., 2017; Carnicer, Stefanescu, et al., 2019). The heat-wave event of late June of 2019 was preceded by an anomalous dry period. Standardised Precipitation Evapotranspiration drought indices (SPEI; extracted from SPEIbase v2.6; <https://spei.csic.es/database.html>) indicated a sustained preceding drought period, reporting  $-1.8$  SD units in June SPEI 6 relative to the long-term mean (1950–2010). The preceding period of soil drought possibly interacted with

the late June extreme heatwave event, affecting soil energy balance during the event (thermal amplification processes, see Table S1 for a precise definition).

### 2.1.2 | Altitudinal patterns of herbivore damage, sapling recruitment and forest structure

To assess the abundance of recruits and its spatial variability we established a total of 36 linear transects covering the whole topographic gradient (establishing six transect replicates per topographic band, perpendicular to the elevational gradient, see Tables S2 and S3; Figure S1). Tree sapling recruits and adult individuals were categorised in four size categories following the Spanish Forest National Inventory classification (i.e. R1–R4 for saplings and SC1–SC4 for adult trees; Table S2; Carnicer et al., 2014; Coll et al., 2013). Changes in tree density (individuals/ha) across the topographic bands A1–A6 were assessed for each diametric class for holm and sessile oak, applying linear, loess and polynomial models. Significant differences between topographic bands were evaluated applying Tukey–Kramer tests. To assess recruitment success in the forest for *Q. petraea* and *Q. ilex* we calculated Recruit/Adult indices (Table 1A) in all the topographic bands of the gradient.

Two independent indicators of mammal herbivore damage on saplings were evaluated [terminal twig damage by roe deer (TTD), and rooting damage by wild boar (RD), Table S4]. The patterns of herbivore damage along the elevational gradient were evaluated (topographic bands A1–A6). In each topographic band, six parallel transects were established quantifying terminal twig damage (TTD) in all recorded saplings for R1 and R2 size classes. For the assessment of soil surface affected by wild boar rooting (RD), three plots (1 m<sup>2</sup>) were randomly measured in each transect (i.e. 18 plots per each topographic band). Table S3 summarises the species-specific transect length and width applied for each tree species and size category (*Quercus petraea*, *Quercus ilex*). Terminal twig damage (TTD) in tree saplings has been previously applied as a reliable indicator of herbivore activity in roe deer populations (Partl et al., 2002). In the case of wild boar populations in the study area, acorns and the underground parts of plants (roots, bulbs and rhizomes) constitute an important fraction of the diet (Giménez-Anaya et al., 2020). In this regard, indicators of rooting activity (RD) in the soil provide a good proxy of the spatial variability of damage by wild boar populations (Bueno et al., 2009, Table S4).

### 2.1.3 | Resilience indices, secondary tree growth and relationships with climatic conditions

We applied a suite of forest resilience indices to contrast, along the topographic gradient, the observed responses of secondary growth of *Q. petraea* in climatically exposed and climatically buffered areas (Carnicer, Domingo-Marimon, et al., 2019; Lloret et al., 2011). The indices were applied to dendrochronological samples of the forest (see below, Table S5; Figure S2). As specified in Table 1B, we applied both short-term resilience indices (Lloret et al., 2011) and multidecadal

**TABLE 1** A summary of the recruitment success indices (A) and the resilience, resistance and recovery indices (B) applied in the study of the trends of secondary growth in declining and non-declining areas of the rear edge forest. A detailed mathematical description for each index is provided in Table S6

Index	Type	Description	Reference
<b>(A) Recruitment success indices</b>			
$R_{sp}/A_T$ ratio (Recruit/Adult ratio)	S	Ratio of the density of recruits of a focal tree species ( $R_{sp}$ ) relative to the density of multiple tree species ( $A_T$ ) of the dominant trees inhabiting the canopy	This paper
$R_{sp}/A_{sp}$ ratio (Specific Recruit/Adult ratio)	S	Ratio of the density of recruits of a focal species ( $R_{sp}$ ) relative to the density of a single tree species ( $A_{sp}$ ) of the dominant trees inhabiting the canopy	This paper
<b>(B) Secondary growth resilience indices</b>			
$R_S$ (Resilience)	S	Capacity to reach pre-disturbance performance levels. Ratio between the performance after and before disturbance	Lloret et al. (2011)
$MR_S$ (Multidecadal resilience)	M	Resilience index relative to a reference period before the onset of forest decline. The same reference period is used for multiple drought events	This paper
$MRC_{FW}$ (Multidecadal resistance–resilience curve (fixed window))	M	Multidecadal change in resistance and resilience. Beginning at the drought year $D$ , a sequence is calculated such that, for each year $y$ , the growth of a period $w$ from $y$ is divided by the growth of a reference period	This paper. Carnicer, Domingo-Marimon, et al. (2019)
$MRC_{IW}$ (Multidecadal resistance–resilience curve (increasing window))	M	Multidecadal change in resistance and resilience. Beginning at the drought year $D$ , a sequence is calculated such that, for each year $y$ , the growth from $D$ to $y$ is divided by the performance during a reference period	This paper. Carnicer, Domingo-Marimon, et al. (2019)
$R_C$ (Recovery)	S	Ability to recover relative to the damage experienced during disturbance. Ratio between performance after and during disturbance	Lloret et al. (2011)
$MR_{CFW}$ (Multidecadal recovery curve (fixed window))	M	Recovery relative to the growth observed during a severe drought event. For each year $y$ after the drought, the difference between the growth of a period $w$ beginning at $y$ and of the drought is divided by this last term	This paper. Carnicer, Domingo-Marimon, et al. (2019)
$MR_{CIW}$ (Multidecadal recovery curve (increasing window))	M	Recovery relative to the growth observed during a severe drought event. For each year $y$ after the drought, the difference between the growth from the first year to $y$ and of the drought is divided by this last term	This paper. Carnicer, Domingo-Marimon, et al. (2019)
MD (Multidecadal decline)	M	Observed actual growth relative to a reference period before the decline	This paper
$R_T$ (Resistance)	S	Reversal of the reduction in ecological performance during disturbance. Ratio between the performance during and before the disturbance	Lloret et al. (2011)
$MR_T$ (Multidecadal resistance)	M	Resistance index relative to a reference period before the onset of forest decline	This paper
GRT (Growth recovery time)	S	Duration (in years) starting in the drought year until reaching the pre-drought growth levels again. Recovery period	Thurm et al. (2016)
MGRT (Multidecadal growth recovery time)	M	Duration (years) starting in the drought year until reaching the levels of growth before the onset of forest decline	Modified from Thurm et al. (2016)
TGR (Total growth reduction)	S	Cumulative growth reduction in the drought year plus all years in the recovery period	Thurm et al. (2016)
MTGR (Multidecadal total growth reduction)	M	Cumulative growth reduction in the drought year plus all years in the multidecadal recovery period	Modified from Thurm et al. (2016)
AGR (Average growth reduction)	S	Ratio of total growth reduction divided by the recovery period. Annual mean of growth reduction during the recovery period	Schwarz et al. (2020)
MAGR (Multidecadal average growth reduction)	M	Ratio of multidecadal total growth reduction divided by the length of the multidecadal recovery period	Modified from Schwarz et al. (2020)

(Continues)

TABLE 1 (Continued)

Index	Type	Description	Reference
ARR (Average recovery rate)	S	Magnitude of growth reduction in the drought year (i.e. $1 - R_T$ ) divided by the length of the recovery period. How much growth is averagely recovered each year of the recovery period	Modified from Schwarz et al. (2020)
MARR (Multidecadal average recovery rate)	M	Magnitude of growth reduction in the drought year (i.e. $1 - MR_T$ ) divided by the length of the multidecadal recovery period	Modified from Schwarz et al. (2020)
PARR (Percental average recovery rate)	S	Average recovery rate relative to the growth reduction in the drought year. Percentage of the lost growth that is averagely recovered each year of the recovery period	Modified from Schwarz et al. (2020)
PMARR (Percental multidecadal average recovery rate)	M	Multidecadal average recovery rate relative to the growth reduction in the drought year. Percentage of the lost growth that is averagely recovered each year of the multidecadal recovery period	Modified from Schwarz et al. (2020)

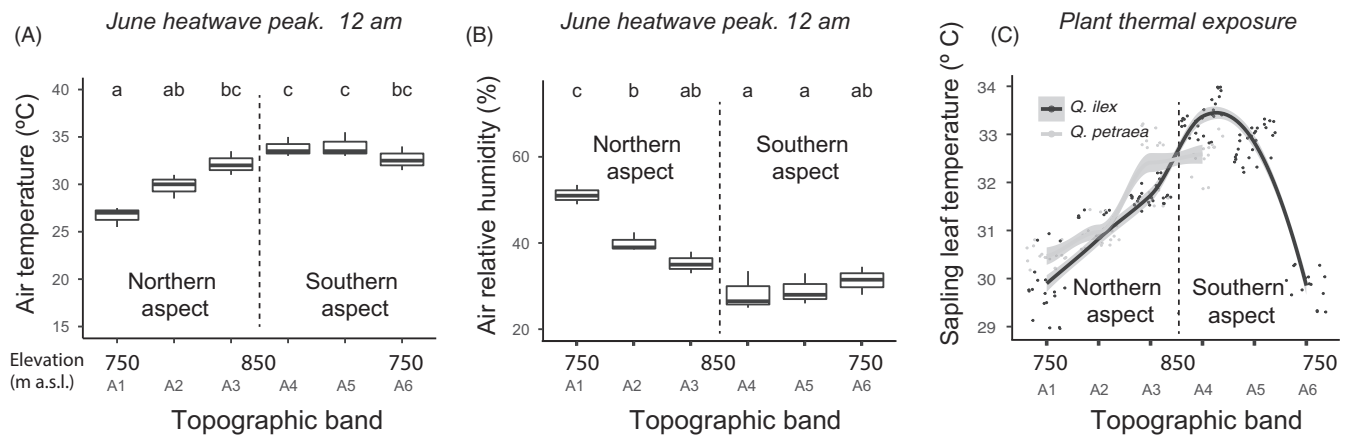
resilience indices (Carnicer, Domingo-Marimon, et al., 2019, Figure 1F). A total of 20 indices were calculated, including resistance, recovery and resilience indices (Table 1; Table S6). Note that while most indices reported an averaged annual value of forest resilience, some of them specifically provided an integrated value for a larger, interannual period of time (Table 1B). Table S6 provides a detailed mathematical description for each of the indices. An R code facilitating the calculation of this integrated suite of indices is provided in the Supplementary file 1 (Table 1; Table S6). The analysis of microclimatic time series (i.e. temperature–humidity 25-cm height LASCAR sensors data) indicated that the two lowland topographic bands of the forest located in northern slopes (i.e. A1–A2, valley area in Figure 1B) were significantly buffered during extreme heatwave events. Over the course of the heatwave event these lowland bands experienced significantly lower extreme summer temperatures and higher air humidity values relative to higher topographic bands inhabited by *Quercus petraea* [ $R^2 = 0.67$ ,  $p < 0.0001$  (lower midday June temperature);  $R^2 = 0.69$ ,  $p < 0.0001$  (higher midday air humidity)]. This different exposure was assessed analysing LASCAR sensor data for June 2019. To contrast forest growth trends in these climatically exposed and buffered topographic bands two complementary approaches were implemented. First, for selected dominant trees of *Q. petraea* located in either valley areas (A1–A2 bands) or ridge areas (A3–A4) we obtained dendrochronological time series (see Table S5). We compared growth trends in these two areas exposed to significantly different thermal regimes (Figure 1C,D). We applied the recommended optimal sample size effort indicated for *Q. petraea* in previous dendrochronological studies (following Mérian & Lebourgeois, 2011), achieving robust EPS values ( $>0.96$ , Table S5). Two cores per adult tree were sampled using a 5 mm diameter increment borer, each corresponding to the eastern and western direction respectively. Samples were processed, dried, mounted and glued to wood supports. Cores were visually dated with a binocular microscope. Tree ring-width series were calculated for each forest area using the software WinDENDRO (Regent Instruments Inc. 2019) and dPLR package in R (Bunn et al., 2020). Cross-dating was carried out using the software COFECHA (Holmes, 1983). From the selected series, Basal Area Increment was calculated as a proxy of secondary tree growth. To analyse the climatic relationships with tree growth trends, climatic data for the study site were

obtained from the NERC Data Repository for Atmospheric Science and Earth Observation (<https://catalogue.ceda.ac.uk/>). Standardised Precipitation Evapotranspiration drought indices (SPEI) were obtained from the dataset SPEIbase v2.6 (<https://spei.csic.es/database.html>). The relationship of secondary growth (Basal Area Increment, BAI, dependent variable) with climatic variables was assessed using both GLM and GLMM approaches, analysing significant associations with monthly temperatures and precipitation. In GLM analyses, we applied a model selection approach (AIC criterion) and selected the strongest climatic predictors, using the functions *glm* and *step* from the *stats* package, and used as the response variable the group-averaged BAI (for valley and ridge areas). For GLMM analyses, we used the R package *lme4*, applying a Gaussian family with identity link. In this case, individual-level BAI was the response variable and we added tree identity as a random factor. All statistical and dendrochronological analyses were done using R 4.0.3 (R Core Team, 2020). A period of continued forest decline in secondary growth was detected (1980–2019), preceded by a previous period of more stable growth (1960–1979). We analysed non-stationary effects of the climatic variables on growth for these two contrasting time periods (e.g. Carnicer, Domingo-Marimon, et al., 2019). The analyses of resilience indices focused on the major periods of drought detected in each decade in the period of forest decline (1980–2019), corresponding to the summers of 1982, 1999, 2006 and 2015 (Figure S3). In addition, we developed a detailed analysis of the relevant time-scales for secondary growth of summer drought events, applying monthly SPEI indices of variable time length for all seasons (1–24 months, summarised in Figure S4). Complementarily, the relationships of BAI with SPEI drought index at multiple monthly time-scales were also assessed (1, 3, 6, 12 and 24 months, results not shown).

### 3 | RESULTS

#### 3.1 | Observed variability in microclimatic conditions

During the heatwave event, we observed strong, significant differences in climatic exposure across microsites along the elevational



**FIGURE 2** Climatic exposure of tree saplings during the extreme heatwave event of June 2019. (A) Midday temperature and (B) Midday relative humidity recorded by LASCAR EL-USB-2 temperature–humidity sensors in the understorey. In the panels A and B different lower case letters indicate significantly different exposure between topographic bands (A1–A6) in Tukey–Kramer tests ( $p < 0.0001$ ). (C) Observed thermal exposure in leaf saplings (midday values, 12–14:00 hr) during the peak of the heatwave event (27 June). A spline fit is illustrated describing the observed variation in leaf temperature of the saplings of *Quercus petraea* (grey line) and *Quercus ilex* (black line)

gradient, both in thermal and air humidity values (Figure 2A,B) and in leaf sapling temperature (Figure 2C). Figure S5 reports thermal exposure values observed at midnight. The observed temporal dynamics of temperature and humidity conditions in the topographic bands A1–A6 are described in Figure 1C,D. During the extreme heatwave event, the thermal exposure of oak saplings below the understorey was largely buffered when compared to control sites in open forested gaps completely exposed to direct sun radiation, which were not successfully colonised by oak saplings (Figure 3). Significant effects of local thermal amplification and thermal buffering processes were detected, determining sapling exposure during the heatwave event (Figure 3). No significant differences of canopy cover were detected across the topographic bands dominated by *Q. petraea* in the period of the heatwave event (A1–A4; Tukey–Kramer test,  $F = 1.28$ ;  $p = 0.28$ ). Tree cover was elevated in most areas of the forest (>65%–85%), and consequently understorey temperatures during the heatwave were non-strongly linked to minor variations in tree canopy cover percentage (Tables S7 and S8). However, a high percentage of *Q. ilex* treelets in the understorey was associated with local thermal cooling patterns (Table S8; Figure S6).

### 3.2 | Patterns of recruitment and herbivore damage in *Quercus ilex* and *Quercus petraea*

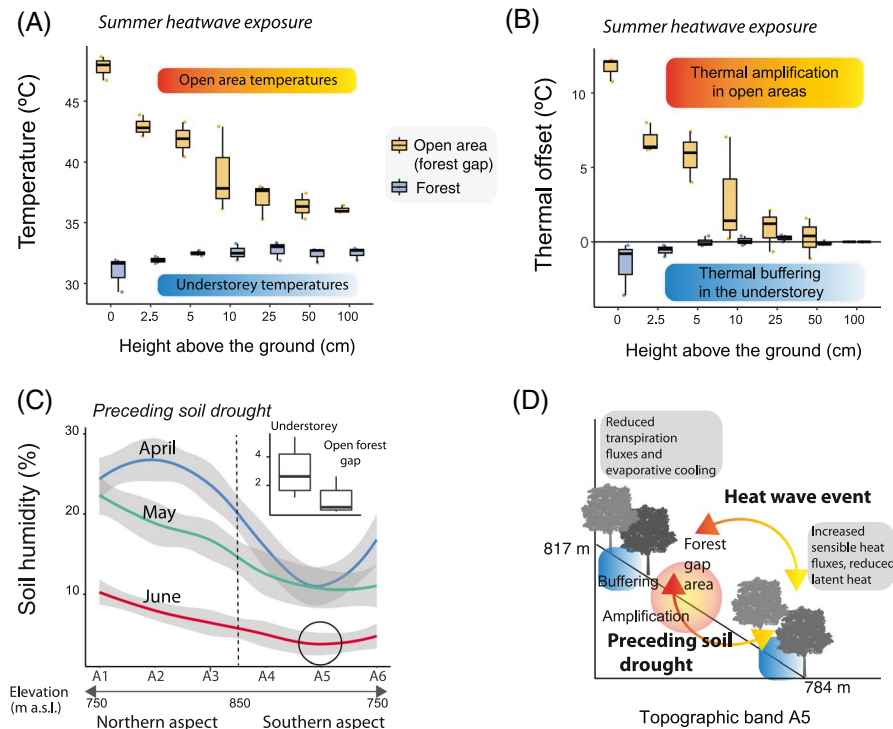
The topographic gradient was associated with contrasting patterns in the abundance and distribution of tree species, with adult individuals of *Q. petraea* clearly dominating in northern topographic bands characterised with milder thermal regimes. In contrast adult individuals of *Q. ilex* were significantly more abundant in southern topographic bands (Figure 4A). While tree saplings of *Q. ilex* were distributed across the whole altitudinal gradient with elevated densities, saplings of *Q. petraea* were abundant only in the topographic bands A1–A4 and were rarely recorded in the southern aspect (Figure 4B; Figure S7).

We observed a significantly negative recruitment trend in *Q. petraea*, showing a strong decrease in the abundance of recruits between consecutive recruit size classes (Figures 4C and 5A). In contrast, *Q. ilex* showed sustained recruitment trends and non-significant differences were observed between size classes R1 and R2 (Figure 5B). Recruitment decrease in *Q. petraea* saplings of size R2 was coherent with the observed high rates of predation of deciduous oak saplings by roe deer (terminal twig damage, Figure 5C; Figure S8). A sustained increase in herbivore pressure due to significant increases in wild boar and roe deer abundances has been observed in the area of study (Figure S9, Rosell et al., 2019). The rooting damage by wild boar was spatially concentrated and dominant factor in river bed and trail areas (Figure S10).

### 3.3 | Contrasting patterns of tree growth and resilience between climatically exposed and buffered areas

The time series of Basal Area Increment (BAI) of *Q. petraea* along the topographic gradient showed contrasting declining and non-declining trends in different areas of the rear edge (Figure 6A). Since the 1980s a divergent, heterogeneous spatial trend in secondary growth was observed, characterised by significant declining growth rates in the more thermally exposed mountain ridge areas [A3–A4 bands] and positive growth trends in the valley areas [A1–A2 bands]. These divergent long-term trends in secondary growth were more efficiently captured by multidecadal resilience indices (Figure 6B,C; Table S9; Figures S11–S14). As illustrated in Figure 6B, ridge areas showed a significant reduction in multidecadal resilience values in the last decades (i.e. 1999, 2006, 2015 drought events) when compared to the observed impacts on resilience in the 1980s. Moreover, the multidecadal resilience index was significantly lower in ridge areas relative to valley areas (asterisks in Figure 6B). Resilience curves ( $MRC_{FW}$ ) also indicated a sustained decrease in resilience in the last





**FIGURE 3** Contrasting midday thermal exposure in areas buffered by the forest canopy and a control area without canopy cover (forest open gap, topographic band A5). Thermal measurements were made in the southern aspect (A5) during the extreme heatwave event of June 2019 using portable thermocouples (panels A and B). A description of observed soil humidity dynamics across the whole topographic gradient is provided in panel C (April–June period). (A) Observed thermal variability in A5 in two spatially adjacent areas [open forest gap (brown)/forested area (blue)] in relation to the distance to the ground. (B) Observed trends of thermal offset (see Table S1 for a definition), describing amplification and buffering effects relative to air temperatures measured at 1 m height above the ground in the same focal point. (C) Observed changes in soil humidity in the drought period preceding the heatwave event (April–June period, for all topographic bands). The INSET graphic highlights observed significant differences (One-way ANOVA,  $R^2 = 0.23$ ,  $p < 0.01$ ) in soil humidity of June between the control forest gap and forest understorey of the band A5 (i.e. southern aspect, 784–817 m). Soil moisture in A5 was extremely low in June (showing a mean value of  $1.18 \pm 0.35\%$  in gap areas, and  $2.88 \pm 0.52\%$  in adjacent understorey areas covered by *Quercus ilex* trees). (D) A visual scheme summarising the dependence of sapling thermal exposure on the preceding soil drought period (panel C) and the cooling effects produced by the canopy structure (panels A and B). Blue circles represent canopy cooling effects reported in panels A and B. The orange circle represents the extreme thermal exposure observed in areas without canopy cover and significantly lower soil humidity (reported in panels A–C). Red arrows schematically represent the possible interactions between the documented preceding drought period (panel C) and the late June heatwave event, determining thermal exposure on saplings due to vegetation and other land-atmospheric feedbacks (reviewed in Table S1)

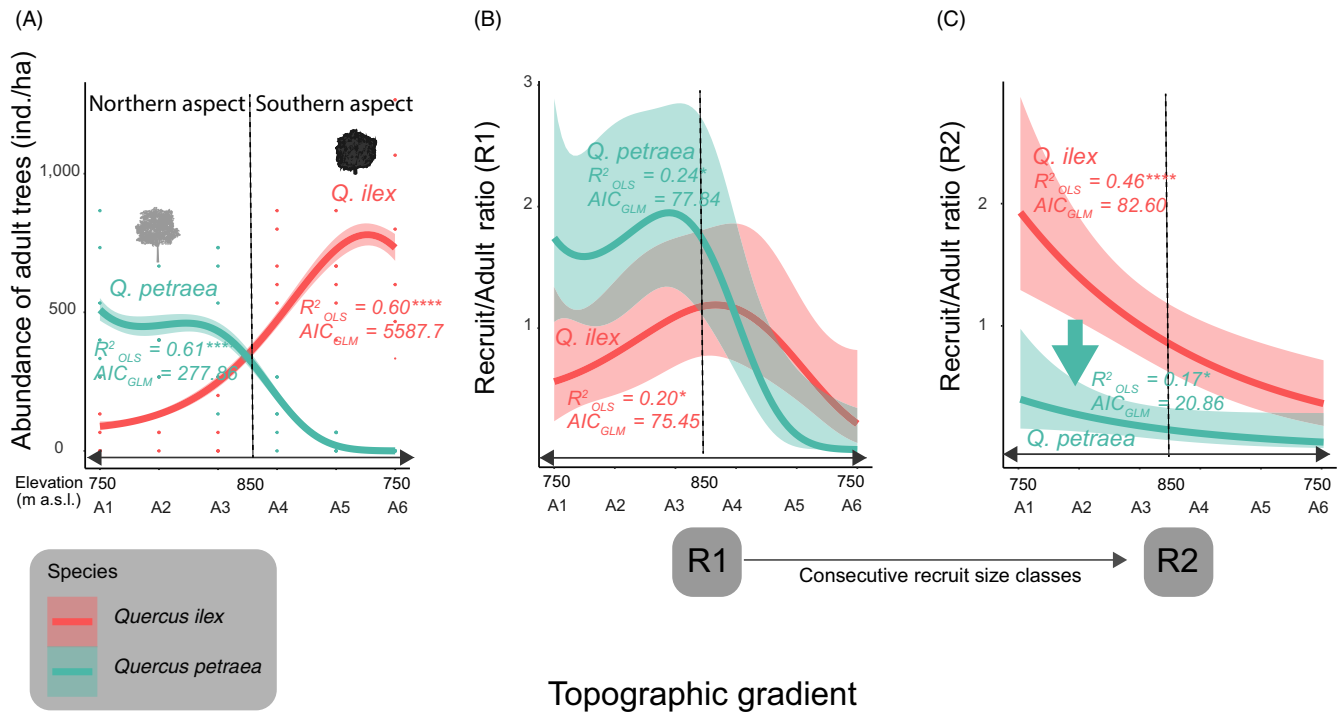
decades in climatically exposed areas (Ridge, Figure 6C; Figure S13). Short-term resilience indices were not fully capturing the observed declining trends (Figure S11; Table S9), but provided complementary information on short-term recovery capacity. The observed correlations between all the short-term and multidecadal indices listed in Table 1 are summarised in Figure 6D and Figure S14. The relationships indicate that multidecadal and short-term indices provide qualitatively different and complementary information on forest resilience (green arrow in Figure 6D).

Variable non-stationary effects of climatic variables were detected between the contrasting periods of forest growth [stable period (1960–1979); declining period (1980–2018)] in GLM and GLMM analyses (Table 2, Tables S10–S12). In the first period positive effects on secondary growth of warm winter and spring temperatures were the dominant factors. In contrast, during the warmer period (1980–2018), the negative effects of climatic variables linked to

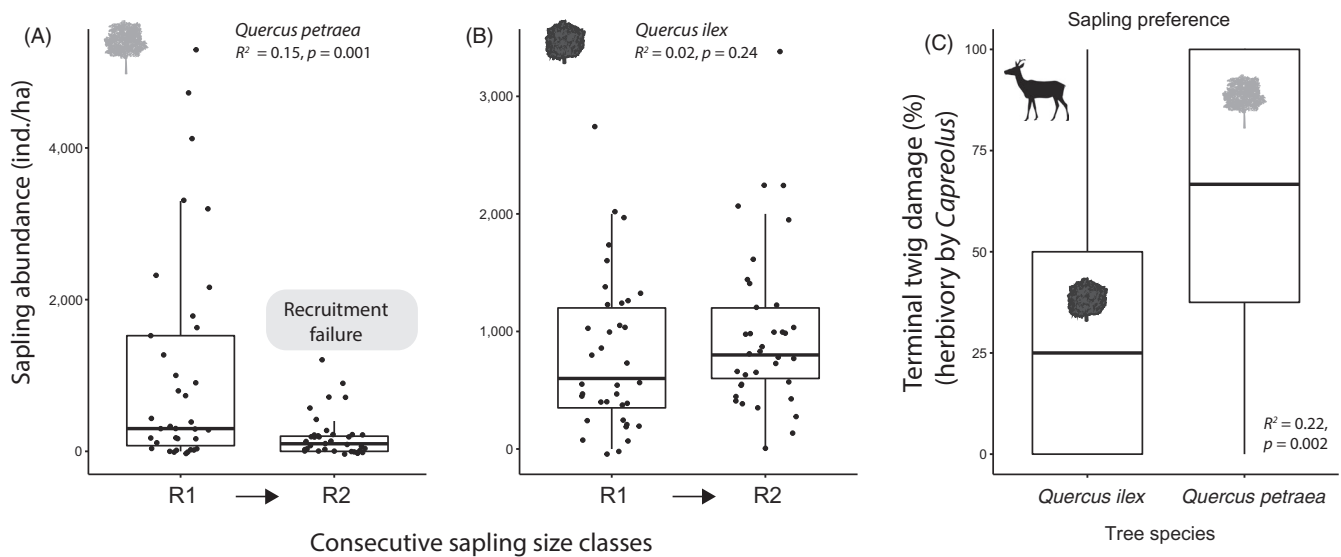
summer drought (June rains and temperatures) were dominant and explained a larger fraction of growth variability (Table 2; Figure S15). The observed negative effects of summer drought and positive effects of winter and early spring temperatures on secondary growth are fully consistent with previous detailed ecophysiological studies of the determinants of secondary growth in this species (Bréda & Granier, 1996, see the discussion for further details).

## 4 | DISCUSSION

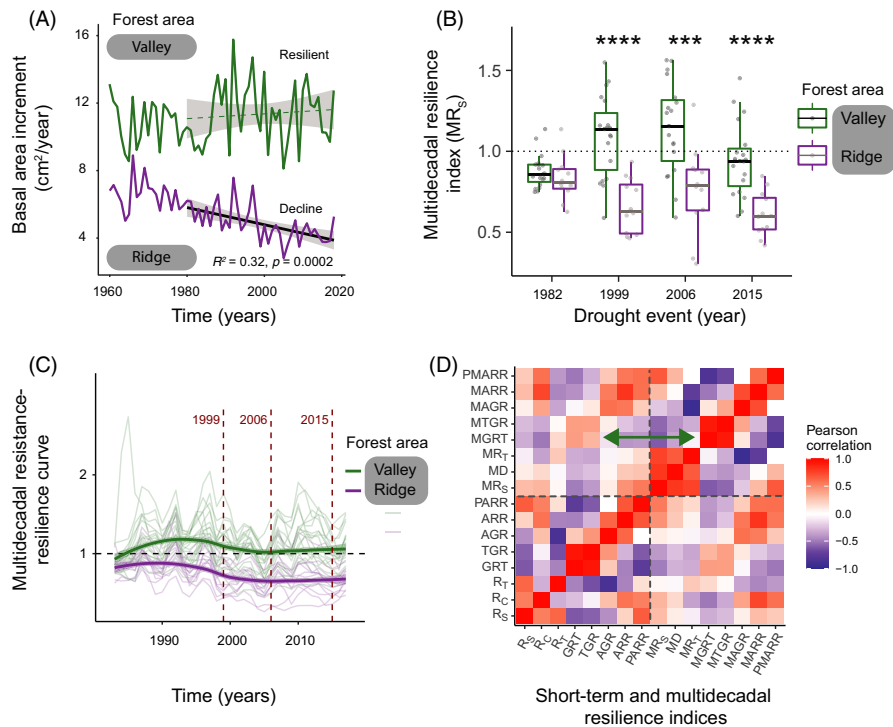
We have applied a diverse suite of 20 forest resilience indices to assess intra-population trends in an endangered rear edge population of *Q. petraea*. As suggested by recent works (Capdevila et al., 2020; Carnicer, Domingo-Marimon, et al., 2019; Ingrisch & Bahn, 2018; Lloret et al., 2011; Schwarz et al., 2020; Thurm et al., 2016), our results



**FIGURE 4** Effects of topographic heterogeneity on adult tree and sapling abundance of *Quercus* trees in the studied rear edge forest. (A) Adult tree abundance for *Quercus petraea* and *Quercus ilex* across the topographic gradient (including the larger size categories SC2, SC3 and SC4). Two- and three-order polynomial fits were applied, fitting generalised linear models (GLM with a Poisson distribution and log link) and ordinary least squares (OLS) models. GLM fits are illustrated, and the associated Akaike information criterion (AIC) is indicated. Complementarily, the variance ( $R^2$ ) and significance (asterisks) reported by OLS polynomial fits are also indicated (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\*\* $p < 0.0001$ ). (B) Observed changes in recruit/adult ratio ( $R_{sp}/A_T$  ratio, Table 1A) along the topographic gradient for the recruit size class R1. (C) Observed changes in recruit/adult ratio for the recruit size class R2. The green arrow highlights the sharp reduction on recruitment success in *Q. petraea* between consecutive size classes (R1 and R2)



**FIGURE 5** Observed trends in sapling recruitment success, and differences in herbivore damage by roe deer *Capreolus capreolus*. (A) Observed recruitment failure in R2 saplings of *Quercus petraea* across two consecutive size classes (R1–R2). (B) Sustained recruitment success in *Quercus ilex*. (C) Observed differences in terminal twig damage associated with roe deer herbivory between *Q. petraea* and *Q. ilex*. A one-way analysis of variance (ANOVA) is provided in the three panels



**FIGURE 6** Forest secondary growth and resilience trends. (A) Time series (1960–2020) of secondary tree growth represented by Basal Area Increment ( $\text{cm}^2/\text{year}$ ) for the mountain ridge (violet line, declining strand) and valley areas (green line, resilient stand), showing the contrasting tendencies observed since the 1980s in climatically exposed and buffered areas of the rear edge. (B) Observed intra-population variability in forest resilience indicators, applying in this case the multidecadal resilience index (MRs, Table 1) for the selected drought events. MRs is calculated for the tree population at the ridge (violet box plots) and valley areas (green, resilient areas of the forest). A one-way ANOVA test is provided comparing MRs mean between ridge and valley areas (\*\* $p < 0.001$ ; \*\*\*\* $p < 0.0001$ ). In the illustrated results reference time period considered for the resilience analysis is a 2-year period (1979–1980). For other reference periods the results were qualitatively the same (see Supporting Information). (C) Observed trends in the multidecadal resistance-resilience curve ( $\text{MRC}_{\text{FW}}$ ), with a fixed window of 2 years, illustrating the diverging trends between the valley and ridge areas (green and violet lines). Thin lines illustrate the trends for individual trees in both areas. (D) Observed Pearson correlations between all the analysed resilience indices

**TABLE 2** General Linear models of secondary tree growth, testing for the effect of climatic variables. BAI (Basal Area Increment) was used as a measure of secondary tree growth. Forest area indicates the location of the stand in the topographic gradient

Time period	Forest area	Predictor	Estimate	SE	t value	Pr ( $> t $ )	$R^2$	p-value
1960–1979	Ridge	TApr	24.87	15.75	1.58	0.11	0.13	0.001
		<b>TJan</b>	<b>37.77</b>	<b>11.47</b>	<b>3.29</b>	<b>0.001</b>		
		PreJun	0.81	0.50	1.61	0.11		
	Valley	<b>TApr</b>	<b>106.56</b>	<b>24.94</b>	<b>4.27</b>	<b>&lt;0.001</b>		
		<b>TJan</b>	<b>79.73</b>	<b>18.17</b>	<b>4.39</b>	<b>&lt;0.001</b>		
		PreJun	1.45	0.79	1.83	0.069		
1980–2018	Ridge	TJun	-35.83	8.67	-4.12	<0.001	0.64	<0.001
		<b>PreJun</b>	<b>1.57</b>	<b>0.34</b>	<b>4.66</b>	<b>&lt;0.001</b>		
	Valley	<b>PreJun</b>	<b>3.49</b>	<b>0.70</b>	<b>4.98</b>	<b>&lt;0.001</b>		

Bold letters highlight the most significant predictors detected.

indicate that resilience trends are best captured applying multiple indicators. In our case study, we focused on capturing and integrating both multidecadal and short-term variability in resistance, resilience and recovery capacity (Table 1, Table S6). We observed that in forest stands affected by long-term declines and non-stationary climatic effects,

multidecadal resilience indices and the application of multiannual resilience curves (Figure 6; Table S9) provide useful descriptors of forest vulnerability to climate warming in its intra-population variability, complementing in this way assessments based in the analysis of short-term resilience indicators (Gazol et al., 2017, 2018; Lloret et al., 2011).

We observed that forest resilience indices differed in areas affected by contrasting levels of thermal exposure during extreme heatwave events. Thermal buffering and amplification effects during extreme heatwave events remain still poorly described in Mediterranean ecosystems and elsewhere (Carnicer, Stefanescu, et al., 2019; Frey et al., 2016; Schwaab et al., 2020). In this paper we report a first detailed description of the modulation of the thermal exposure in tree saplings during an unprecedented extreme summer heatwave event, based on detailed field measurements (van Oldenborgh et al., 2019; Zhao et al., 2020). Variability in thermal exposure during the heatwave was clearly linked to local topography and vegetation cover effects (Figures 1C, 2 and 3). In a relatively short altitudinal distance, we measured contrasting microclimatic conditions. Particularly, during the heatwave event the highest air temperature in the understorey and the lowest air relative humidity coincided with the forest sections closest to the ridge (Figure 2A–C). Microclimate variability along the gradient was further intensified during a summer heatwave relative to previous colder periods of the summer (Figure 1C,D). Because an increase in summer heatwave frequency is very likely for the Mediterranean region in the coming decades (Guiot & Cramer, 2016; IPCC, 2018), the effect of topography might exacerbate within-site variability and modulate impacts of extreme events on tree demographic performance (Rita et al., 2020). Climate buffering effects of forest canopies are well-known (De Frenne et al., 2021; Zellweger et al., 2020), although they depend on water availability and thus can vary intra- and inter-annually (Carnicer, Stefanescu, et al., 2019; Davis et al., 2019; von Arx et al., 2013). Microclimatic variability seems to be relevant in the studied rear edge forest, since *Q. petraea* recruitment success was restricted to mesic, northern slope microsites and secondary growth and resilience were also largely affected by topographical variability (Figure 6). We detected greater vulnerability and limited resilience of the tree stand situated in the higher and more exposed part of the topographic gradient, in line with previous studies highlighting the key role of local-scale topography in determining thermal exposure (Bramer et al., 2018; Graae et al., 2018; Lenoir et al., 2013; Scherrer & Körner, 2010). In addition, we detected species-specific cooling effects of some species (*Q. ilex*) in microclimatic measurements (Table S8; Figure S6). This suggests that the current expansion of treelets of *Q. ilex* and other similar oak species in the understorey of most Mediterranean forests, which is linked to the widespread advance of forest succession over extensive areas (Carnicer et al., 2014), might be altering the patterns of microclimatic exposure at the regional scale.

Our results indicate that rear edge tree populations are vulnerable to the combined effect of both global change-induced abiotic and biotic stressors. Rear edge populations often occur in climate refugia, but their persistence can be often restricted or facilitated by biotic interactions (Hampe, 2004; Hampe & Jump, 2011). Among abiotic factors, climate is often recognised as the most relevant factor limiting species distributions, including trailing and rear edge areas (Harsch & HilleRisLambers, 2016; Normand et al., 2009; Pearson &

Dawson, 2003). However, in our case study we found that mammal herbivory (i.e. a biotic stressor) largely determined the fine-scale patterns of a key life-history stage (i.e. sapling recruitment). Due to these biotic factors, recruitment success largely differed between these competing tree species (Figure 5), characterised by contrasting climatic niches, and by spatially overlapped distributions in a narrow forest ecotone. This highlights that in order to predict the performance and assess the resilience of rear edge populations to global change, integrative studies considering multiple drivers are more likely to capture all relevant demographic processes.

We also found high spatial heterogeneity in the response to climatic factors in the rear edge, with positive growth responses in climatically buffered sections of the topographic gradient (valley areas), which contrasted with the negative trends observed in climatically exposed areas of the gradient (Figure 6). The response of most resilience indices in *Q. petraea* was strikingly different across a gradient of tens of metres along the ecotone. Within the same population and inside a rear edge area, climatically buffered microsites were associated with greater resilience and recovery capacity (Figure 6; Figure S13). Our results show that within-population variability in growth and resilience can be really high and that not all trees might be equally able to cope with future warmer and drier conditions. The difference in growth and resilience between ridge and valley *Q. petraea* trees has been progressively exacerbated since the 1980 (Figure 6). Trees in the valley area maintained a positive growth trend, achieving growth rates also reported for other non-stressed stands at the same latitude, but presenting lower growth rates than those observed in northern populations of the same species (Bréda & Granier, 1996; Martínez-Sancho et al., 2018). In sharp contrast, trees in the ridge area have been affected by an increasing water deficit, possibly due to a post-1980 climatic shift to warmer and drier conditions reported in the Eastern Iberian Peninsula (Carnicer, Domingo-Marimon, et al., 2019). This can be concluded from the climate-growth model (Table 2), which clearly indicates more significant negative effects of summer drought and summer temperatures after 1980. Climate impacts on tree growth have shifted from positive effects of warm late winter and early spring temperatures (1960–1970s) to strong limitations by warm and dry summer effects over the last decades (Table 2). These climate-induced trends are fully consistent with previous studies of secondary drought in *Q. petraea* reporting negative effects of summer drought stress and positive effects of late winter and early spring temperatures (Bréda & Granier, 1996; Michelot, Bréda, et al., 2012; Michelot, Simard, et al., 2012). The secondary growth in this species starts prior to budburst and leaf expansion (Michelot, Bréda, et al., 2012; Michelot, Simard, et al., 2012); and almost half of the annual ring can be produced in the spring period (Bréda & Granier, 1996). Although warmer temperatures can promote cambium cell division (Pérez-de-Lis et al., 2017), this process is also limited by water availability (Eilmann et al., 2006). Increased resilience observed in valley trees could be facilitated by topography, promoting soil water storage in lowland areas, and dampening the negative effects of drought for the valley trees (Dymond et al., 2017). Similarly, shallow soils in ridge areas

cannot store as much water as soil further down the valley, promoting limited resilience and recovery capacity in these stands. Resilient trees in the valley appear to be less sensitive to climate than other populations located at the core of the species distribution (Martínez-Sancho et al., 2018). At least a part of the studied rear edge forest appears to benefit from buffering environmental conditions that decouple this stand from macroclimatic fluctuations, matching the definition of a climatic and hydrological refugia (Fan et al., 2020; Lenoir et al., 2017; McLaughlin et al., 2017). In this sense, our findings are in line with those of recent studies reporting higher resistance to drought in rear edge populations, compared to core distribution populations (Muffler et al., 2020; Vilà-Cabrera et al., 2019).

Our findings do not support scenarios predicting rapid, spatially homogeneous distributional shifts and limited resilience in rear edge populations of the Mediterranean biome. These uniform and simple scenarios of massive forest retreat can be often predicted applying climate-envelope species distribution models (SDMs, as discussed in Hampe, 2004; Hampe & Jump, 2011). Our results instead are more supportive of more complex scenarios including spatially heterogeneous responses, characterised with contrasting intra-population trends of forest resilience. Such heterogeneity would be mediated by local thermal buffering and amplification effects, and variable drought stress linked to topographic gradients, soil and land cover variability (Carnicer, Stefanescu, et al., 2019). We provide evidence for a significant within population variation in resilience, emphasising in our case study the relevance of microclimatic variability in the dynamics of rear edge populations. Furthermore, our results also support the existence of non-stationary effects of climate determining forest growth responses (Table 2; Astigarraga et al., 2020; Carnicer, Domingo-Marimon, et al., 2019; Peltier & Ogle, 2020). Finally, as previously mentioned, our results also emphasise an important role of other interacting global change drivers such as imbalanced recruitment due to increased herbivore pressure in locally altered, defaunated trophic networks, that we discuss in detail below.

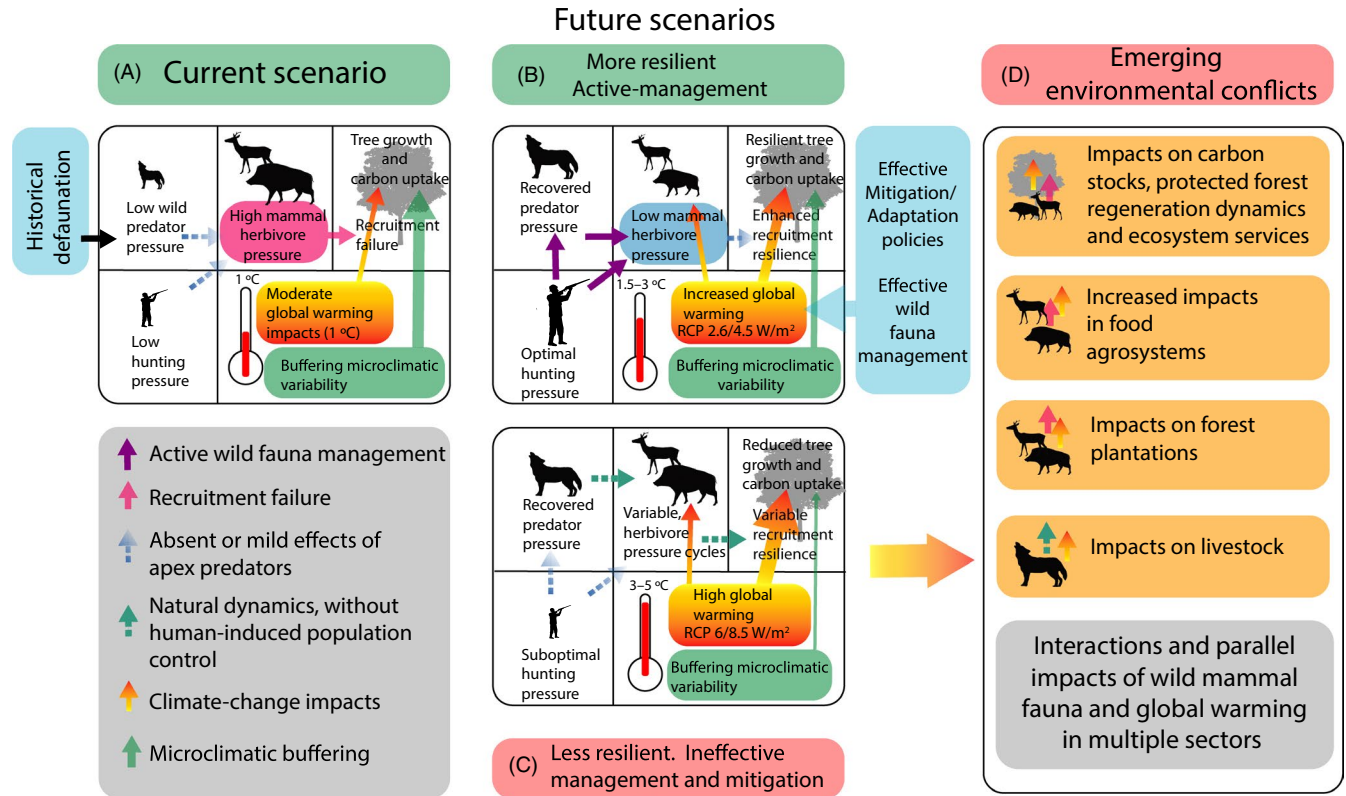
Significant species-specific differences were found in the patterns of tree sapling abundance and recruitment success. Although both *Q. petraea* and *Q. ilex* presented similar recruitment success for the first size class (R1), a larger survival rate in the transient phase from the first to the second class was observed in the evergreen *Q. ilex* species (R2, Figures 4 and 5). This was possibly related to the strong and selective herbivore pressure by roe deer specifically affecting broadleaved oak saplings of *Q. petraea* (Figure 5C), which is consistent with previous studies of selective consumption of tree saplings and dietary preferences in this mammal species (e.g. Partl et al., 2002).

We also observed a spatially clustered pattern of damage by wild boars, which was mainly concentrated nearby river bed and forest trail areas (Figure S10). In these specific areas, the effects of rooting damage by wild boar were dominant and often completely precluded recruitment success in sessile oaks. Wild boar and roe deer are the main ungulate species inhabiting the studied area (Rosell et al., 2019; Torres et al., 2016). Controlling roe deer and wild boar

populations is a major concern and challenging task in the NE Iberian Peninsula (Giménez-Anaya et al., 2020), and increasing hunting pressure in protected areas often fails to effectively regulate population size (Figure S9). Similarly, in the rest of Europe, wild boar populations have grown at rates not matched by human hunting pressure (González-Crespo et al., 2018; Massei et al., 2015). As a result, multiple ecosystem alterations are currently caused by increasing wild boar and roe deer impacts (Barrios-García & Ballari, 2012). Previous studies have also shown a limiting effect of wild boar damage on the recruitment of *Quercus* saplings (Gómez et al., 2003; Gómez & Hódar, 2008).

Figure 7 summarises possible future scenarios for Mediterranean rear edge forest resilience in the next decades, accounting for the mixed effects of climate change warming impacts, altered mammal herbivory and microclimatic variability. The current scenario in our study case is dominated low wild predator pressure and suboptimal human hunting pressure, which ultimately result in a high mammal herbivory pressure and recruitment failure (Figure 7A). These trends co-occur with still moderate but increasing impacts of warming, which affect the forest resilience in non-buffered areas of the forest. We suggest that in the next decades, resilient scenarios will possibly require effective mitigation and adaptation policies to limit climate warming impacts on forests (IPCC, 2018), combined with regional plans for wild mammal management (Figure 7B, violet arrows). In the eastern Iberian Peninsula wolf populations are expected to naturally recover in the following decades, from present very low densities in the area [in the order of 0.0004 ind./km<sup>2</sup>, which contrast with current high regional densities of wild boar (3–15 ind./km<sup>2</sup>) and roe deer (0.5–10 ind./km<sup>2</sup>); Rosell et al., 2019]. Ineffective implementation of climate policies and regional wild fauna management plans would possibly lead to low resilience scenarios for protected and endangered rear edge forests, increasing negative interactions between unregulated wild mammal populations and warming impacts on protected areas and on multiple land sectors in adjacent areas (Figure 7C; Badano et al. 2015; Havlík et al., 2014; Kolström et al., 2011; Kuijper et al., 2019; Martin et al., 2020; Nardone et al., 2010; Rojas-Downing et al., 2017). According to these scenarios, we suggest that forest resilience studies would benefit from combining the analysis of growth resilience relationships and indicators of demographic resilience in different tree life-history stages (reviewed in Capdevila et al., 2020).

We conclude that forest resilience and heterogeneous demographic responses to climate warming are ultimately modulated by the influence of the local environment on individual trees (Levine et al., 2016). Accurate predictions of forest responses to changes in climate would largely benefit, thus, from the integration of local-scale variation of key factors such as microclimatic conditions and biotic interactions, as our results and previous studies support (Lembrechts et al., 2019; Vilà-Cabrera & Jump, 2019; Zellweger et al., 2020). Macroclimate should not be used alone to predict recruitment success and forest resilience in future scenarios because fine-scale microclimate and biotic interactions can be also important factors.



**FIGURE 7** A synthetic summary of multiple scenarios for forest resilience, explicitly considering the complex interactions between global warming impacts, wild fauna management and local microclimatic variability. (A) A synthetic diagram of the current scenario in the studied *Quercus petraea* rear edge forest. (B, C) Future scenarios ranging from low to high atmospheric concentrations of greenhouse gases (Representative Concentration Pathways, IPCC, 2018). The width of the green and orange arrows in panels A, B and C represents the relative magnitude of the expected effects of global warming and microclimatic buffering processes. (D) Emerging combined impacts of global warming and unregulated wild mammal populations on protected forests and adjacent land areas. The arrows in panel D indicate the key ecological and climatic processes involved, according to the grey panel on the left

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## AUTHORS' CONTRIBUTIONS

J.C. designed the research; X.M.-C., J.C., L.B., A.B., M.V.-I., C.R., S.S., E.G., J.P. and T.S. collected the field data; M.V.-I. and J.C. designed and implemented the resilience calculations; J.C., M.V.-I. and A.B. contributed new analytic tools and analysed the data; J.C. wrote an initial draft of the paper and all authors contributed to the final document.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data is available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.vq83bk3t5> (Carnicer, 2021).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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