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# Effects of thinning in a water-limited holm oak forest. Romà Ogaya<sup>1,2\*</sup>, Anna Escolà<sup>1,2</sup>, Daijun Liu<sup>3</sup>, Adrià Barbeta<sup>4</sup>, Josep Peñuelas<sup>1,2</sup> <sup>1</sup>CREAF, Cerdanyola del Vallès, E-08193, Catalonia, Spain <sup>2</sup>CSIC, Global Ecology Unit CREAF-CEAB-CSIC, UAB, E-08193, Cerdanyola del Vallès, Catalonia, Spain. <sup>3</sup>School of Geography, Earth and Environmenttal Sciences, University of Birmingham Edgbaston, Birmingham B15 2SQ, United Kingdom. <sup>4</sup>INRA, UMR ISPA, F-33140, Villenave d'Ornon, France. \*Corresponding author: Romà Ogaya, Global Ecology Unit CREAF-CEAB-CSIC, Universitat Autònoma de Barcelona, E-08193, Cerdanyola del Vallès, Catalonia, Spain. Tel.: +34-935814036, Fax: +34-935814151, E-mail: r.ogaya@creaf.uab.cat

### Effects of thinning in a water-limited holm oak forest.

#### Abstract

A natural holm oak forest was selectively thinned to test thinning as a tool to reduce tree mortality, increase productivity, and reverse the recent regression of the dominant species (*Quercus ilex*) induced by climate change. Thinning increased aboveground productivity and reduced stem mortality in this Mediterranean forest during four years just after thinning, contributing to the maintenance of forest functioning under changing climatic conditions. *Q. ilex* was the only species positively affected by the thinning: stem growth increased for all stem sizes, and mortality was significantly lower in thinned plots. On the contrary, mortality rates of *Phillyrea latifolia* and *Arbutus unedo* were not significantly lower. Stem growth increased for *P. latifolia* only in the smallest stem-size class. Our results highlight the suitability of selective thinning for improving the forest productivity and ensuring the conservation of Mediterranean coppices. Other benefits of selective thinning, such as a decrease in the risk of fire dispersion and an increase in the water supply for human populations, are also discussed.

- 47 Keywords: carbon sink; climate change; forest dieback; forest management; holm oak;
- 48 Mediterranean forest; selective thinning; tree growth; tree mortality.

#### Introduction

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Air temperatures have already increased globally and are projected to continue to increase in the coming decades, and it has been predicted that the intensity and duration of extreme weather events, such heat weaves, floods, and droughts spells will increase (IPCC, 2018; Wang, Peng, Kneeshaw, Larocque, & Luo, 2012). Higher evapotranspiration rates induced by warmer temperatures coupled to slight decreases in precipitation are expected in many areas, such as the Mediterranean Basin, that are already subjected to seasonal drought (IPCC, 2013). Robust climatic models have projected a continuous increase in the severity of warming and drought in the Mediterranean Basin for the coming decades, which could have severe impacts on carbon (C) sinks in forest ecosystems and alter regional C budgets (Bates, Kundzewicz, Wu, & Palutikof, 2008; Dai, 2013; Reichstein et al., 2013). Moreover, strong relationships between deficits in precipitation and subsequent occurrences of hot extremes have been widely observed (Mueller & Seneviratne, 2012), and higher frequencies of heat waves coinciding with summer drought, higher evapotranspiration, and the subsequent low availability of water are also expected for Mediterranean regions (Fischer & Schar, 2010). Some forested ecosystems in semi-arid and Mediterranean areas are seasonally exposed to drought and may be particularly vulnerable to even slight increases in water deficit, which can reduce tree growth (Ogaya & Peñuelas, 2007; Barbeta, Ogaya, & Peñuelas, 2013) and increase tree mortality (Breshears et al., 2005; Allen et al., 2010; Peng, Ma, Lei, & Peng, 2011; Williams et al., 2013). Forest ecosystems contain large stocks of C and represent important potential C sinks (Pan et al., 2011). Forest ecosystems may mitigate climate change by sequestering C, so the effects of forest management practices on ecosystemic C sinks need to be assessed. Selective thinning is a common practice for improving forest health and productivity (Roberts & Harrington, 2008) and accelerating forest succession (Sullivan & Sullivan, 2016), and the trees remaining after selective thinning generally receive more solar radiation, soil water, soil organic matter, and nutrients, which increase their photosynthetic capacity (Peterson, Seiler, Nawak, Ginn, & Kreh, 1997; Tang, Chambers, Guddanti, & Barmett, 1999; Tang, Qi, Xu, Misson, & Goldstein, 2005; Selig, Seiler, Tyree, 2008; Chang et al., 2016), stem growth (Idol, Morales, Friday, & Scowcroft, 2018; Jiménez, Navarro, Sánchez-Miranda, & Ripoll, 2019), and crown development (Sorg, Urech, Mamadzhanov, & Rehnus, 2016; Valinger, Sjogren, Nord, & Cedergren, 2019). Selective thinning is a common management strategy in Mediterranean forests to increase tree growth and ecosystemic productivity, but selective thinning can also increase the capacity of Mediterranean trees to tolerate drought conditions due to the reduction of stem density and the consequent increase in water availability per stem (Cotillas, Sabaté, Gracia, & Espelta, 2009; López, Gracia, Sabaté, & Keenan, 2009; Chang et al., 2016). Several Mediterranean forests are mainly coppices with high stem densities due to ancient management practices to obtain wood and charcoal, followed by a high number of sprouts per cut stem (Ogaya & Peñuelas 2007). Holm oak (Quercus ilex L.) is a widespread and dominant tree species in subhumid areas of the Mediterranean Basin. Many tall shrub species with lower growth rates but a higher resistance to drought are associated with holm oak forests (Peñuelas, Filella, Lloret, Siscart, & Piñol, 1998; Ogaya & Peñuelas 2003). Higher mortality rates and lower seed production and seedling survival of Q. ilex under future drier conditions could decrease the distribution of this dominant species and favour the associated species that are more resistant to a low availability of water (Peñuelas, Lloret, & Montoya, 2001;

Lloret, Peñuelas, & Ogaya, 2004; Barbeta et al., 2013; Liu, Ogaya, Barbeta, Yang, &

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Peñuelas, 2015). All small stems are cut during selective thinning in Mediterranean forests, so only the largest trees remain, mainly *Q. ilex* trees. Shrub species can thus be completely cut, conferring a competitive advantage to *Q. ilex* in addition to the decrease in stem density.

The main objectives of this study were to test selective stem thinning as a tool to compensate forest dieback and tree mortality in a typical Mediterranean forest and to investigate the interaction between drivers of global change and recent practices of forest management (Doblas-Miranda et al., 2015). We also compared the responses of *Q. ilex* and coexisting species (more resistant to drought conditions) to the experimental selective thinning. We tested these responses in the various species by cutting several small sprouts of individual trees during the selective thinning, so the largest stems of all species remained after thinning.

# **Materials and Methods**

#### Study Site

The study area was on a south-facing slope (25% slope) in the Prades Mountains, Catalonia, northeastern Spain (41°21' N, 1°2' E), at an altitude of 950 m a.s.l. The soil is a Dystric Cambisol over Palaeozoic schist, ranging in depth from 35 to 100 cm. The average annual temperature is 12.3 °C, and the average annual rainfall is 603 mm (data from 1998-2015). Summer drought is pronounced and usually lasts for three months. The vegetation is a very dense multi-stem forest (16616 stems ha<sup>-1</sup>) dominated by *Q. ilex* (8633 stems ha<sup>-1</sup>), *Phillyrea latifolia* L. (3600 stems ha<sup>-1</sup>), and *Arbutus unedo* L. (2200 stems ha<sup>-1</sup>), with an abundance of other evergreen species well adapted to dry conditions

such as *Erica arborea* L., *Juniperus oxycedrus* L., and *Cistus albidus* L. and occasional individuals of deciduous species such as *Sorbus torminalis* (L.) Crantz and *Acer monspessulanum* L. This forest has not been disturbed for 80 years, and the maximum height of the dominant trees is approximately 6-10 m. An automated meteorological station installed at the study site has monitored temperature, humidity, and precipitation since late 1998.

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#### Experimental Design and Tree-growth Data

Three  $15 \times 10$  m plots were delimited at the same altitude along the slope. The plots were thinned at the end of 2011, removing about 20% of the basal area (BA) (Table 1). Another four  $15 \times 10$  m plots from another experiment conducted at the same study site were not thinned for use as controls (Ogaya & Peñuelas, 2007; Barbeta et al., 2013; Liu et al., 2015). Stem size was measured in the winters of 2012 and 2016 in both the thinned and control plots and in late autumn 2011 in the thinned plots immediately before thinning for calculating the percentage BA removed from the plots after thinning. Stem size was calculated from the circumference at a height of 50 cm measured with a metric tape for all living stems of all species with diameters >2 cm. Stem sizes were classified into three categories: small stems (2-6 cm diameter), intermediate stems (6-10 cm diameter), and large stems (>10 cm diameter). BA was calculated for each tree from its stem circumference at 50 cm height, assuming a stem circumference section. The annual rate of stem mortality (m) was calculated as (Sheil, Burslem, & Alder, 1995): m=1-(1-(N<sub>0</sub>- $N_t$ )/ $N_o$ )<sup>1/t</sup>, where " $N_o$ " is the number of stems at the start of the studied period, " $N_t$ " is the number of stems at the end of the studied period, and "t" is the number of years of the studied period.

Aboveground biomass in the plots was estimated from the allometric relationships between tree aboveground biomass (AB) and stem diameter at a height of 50 cm (D50). Q. ilex and P. latifolia trees outside the plots were harvested, their circumferences at a height of 50 cm were measured, and all aboveground biomass was weighed after drying in an oven to a constant weight. The aboveground biomasses of Q. ilex and P. latifolia were estimated from the calculated allometric relationships (lnAB=4.9+2.3 lnD50,  $R^2=0.98$ , n=12, P<0.001 for Q. ilex, and lnAB=4.3+2.5 lnD50,  $R^2=0.97$ , n=13, P<0.001 for P. latifolia). The aboveground biomass of A. unedo was estimated from the allometric relationship previously calculated for the same area by Lledó (1990) (lnAB=3.8+2.6 lnD50,  $R^2=0.99$ , n=10, P<0.001).

#### Leaf Area Index Data

The biomass of leaves was also estimated using allometric relationships between the biomass of leaves in each tree (BL) and its stem diameter at a height of 50 cm (D50), from Q. ilex and P. latifolia trees outside the plots. Their circumferences at a height of 50 cm were measured, and the biomass of all leaves were weighed after drying in an oven to a constant weight. The biomass of leaves in Q. ilex and P. latifolia were estimated from the calculated allometric relationships ( $lnBL=3.5+1.7 \ lnD50$ ,  $R^2=0.91$ , n=12, P<0.001 for Q. ilex, and  $lnBL=1.4+2.4 \ lnD50$ ,  $R^2=0.81$ , n=13, P<0.001 for P. latifolia). The biomass of leaves in A. unedo was estimated from the allometric relationship previously calculated for the same area in [32] ( $lnBL=1.9+2.2 \ lnD50$ ,  $R^2=0.95$ , n=10, P<0.001). For the other species, their AB was estimated from Q. ilex allometric relationships for other tree species, and from P. latifolia allometric relationships for other shrub species.

The total leaf surface was calculated assuming a mean leaf mass per area ratio of 20 mg cm<sup>-2</sup> for *Q. ilex* leaves, and 15 mg cm<sup>-2</sup> for *P. latifolia* and all other species, as it

175 was observed in a previous study conducted in the same site (Ogaya & Peñuelas, 2006). 176

LAI was calculated from total leaf biomass and total leaf surface data for each studied

177 species (Q. ilex, P. latifolia, and A. unedo), and a total LAI data for each plot (Table 2).

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#### Data Analysis

The effect of thinning on BA during the study period (2012-2015) was tested by a general linear model, with thinning, category of stem size, and species as independent factors, and with the mean percentage increase in BA in each plot as a dependent variable. Post hoc tests compared the effects of thinning on increases in BA for each species and stemsize category. Analyses of variance (ANOVAs) were performed to test the effect of thinning on stem mortality and biomass, with thinning and species as independent factors, and with annual mortality rate or the percentage increase in aboveground biomass as dependent variables. Data for the percentage increases in BA and aboveground biomass (p) and annual mortality rate (m) were transformed to  $\arcsin (p)^{1/2}$  and  $\arcsin (m)^{1/2}$  to satisfy the normality assumptions of the ANOVA. All analyses were performed with the Statistica 10 software package (StatSoft Inc., Palo Alto, CA, USA).

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#### **Results**

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# Climatic Data

The climatic conditions during the study period (2012-2015) were typical of Mediterranean areas, with dry and hot summers and moderately cold winters. The weather was especially hot and dry in 2015 and especially humid and cool in 2013. Climatic conditions were average in 2012 and 2014. Mean annual temperature and total annual

precipitation ranged from 11.9 °C and 783 mm in 2013 to 13.3 °C and 355 mm in 2015, respectively (Fig. 1).

## Basal Area and Mortality

Thinning significantly increased BA for *Q. ilex* relative to the control plots (*P*<0.01). In contrast, thinning did not significantly affect BA for *A. unedo* and only tended to increase BA for the smaller stems of *P. latifolia* (*P*=0.09) (Figure 2). BA increased more for small than intermediate and large stems for *A. unedo* and *P. latifolia* but increased less for small than intermediate and large stems for *Q. ilex*. BA increased most for *A. unedo* in the control plots, whereas BA increased least for *Q. ilex*, especially for smaller stems, but also increased more in the thinned plots for all stem sizes. BA increased more for *P. latifolia* than *Q. ilex* for small stems (with also a large increase induced by thinning), but the growth of intermediate stems was similar for *P. latifolia* and *Q. ilex*, with an increase Annual rates of stem mortality were higher for *Q. ilex* than *P. latifolia* and for *P. latifolia* than *A. unedo* in the control plots, but thinning strongly reduced the rate for *Q. ilex* and had no significant effect on the other two species. The annual mortality rate in the thinned plots was therefore even lower for *Q. ilex* than the other two species (Figure 3). Thinning significantly decreased the annual rate of stem mortality for all species together relative to the control plots.

## Aboveground Biomass and Leaf Area Index

Aboveground biomass increased more in the thinned than in the control plots (P=0.02) (Figure 4). The relative aboveground biomass increased more for A. unedo than the other two species in the control plots. The increase in relative aboveground biomass in the thinned plots did not differ significantly between A. unedo and P. latifolia. The difference

in relative aboveground biomass increase between A. unedo and Q. ilex was lower than in the control plots, because thinning increased the biomass for Q. ilex (P<0.01) and P. latifolia (P<0.05) but not A. unedo (Figure 4). In terms of absolute values of aboveground biomass increase, thinning treatment doubled the biomass increase of Q. ilex, while it was not observed any aboveground biomass increase (in absolute values) in the two other studied species induced by thinning (Figure 4). Because of that, in thinned plots the aboveground biomass increment was higher in Q. ilex than in the other two species, while this difference was not observed in control plots.

The percentage of LAI increment was higher in thinned plots than in control plots (P<0.05). The thinning treatment increased LAI in Q. ilex (P<0.01) and P. latifolia (P<0.05), but not in A. unedo (Figure 5). On the other hand, the percentage of LAI increment in Q. ilex was smaller than in P. latifolia and A. unedo in both control and thinned plots.

#### Discussion

Several studies have reported an increase in stem growth (Roberts & Harrington, 2008) and tree C sequestration (Keyser, 2010) induced by selective thinning, in accordance with our results of higher radial growth and biomass in selectively thinned plots, but the response to thinning was species-specific. The ability of tall shrub species such as *P. latifolia* to cope with water stress conferred a competitive advantage over *Q. ilex* at the same study site (Ogaya & Peñuelas, 2007; Barbeta et al., 2013; Liu et al., 2015). Stem growth and biomass increase strongly decreased, and stem mortality strongly increased, for *Q. ilex* but not *P. latifolia* subjected to an experimental drought (Ogaya & Peñuelas,

2007; Barbeta et al., 2013; Liu et al., 2015). The decrease in water availability induced by climate change (IPCC, 2013) is progressively substituting *Q. ilex* with tall shrub species more resistant to drought, such as *P. latifolia* (Liu, Ogaya, Barbeta, Yang, & Peñuelas, 2018). Selective thinning increased *Q. ilex* stem growth for all stem sizes but only increased the growth of smaller *P. latifolia* stems and did not have a significant effect on *A. unedo*. Selective thinning strongly decreased stem mortality for *Q. ilex* but not the other two species. Selective thinning was thus a good strategy of forest management for increasing *Q. ilex* tree growth but also for delaying the progressive replacement of this dominant species by more drought-resistant shrub species. Similar results were observed in other sites around the world, where selective thinning increased stem growth and enlarged the growing season (Idol, Morales, Friday, & Scowcroft, 2018; Jiménez, Navarro, Sánchez-Miranda, & Ripoll, 2019).

Water availability is very important in this water-limited environment, and the selective thinning increased the amount of resources available to the remaining stems and decreased the transpiration surface (LAI) of the forest, as observed in other thinning managements conducted in other forests (Valinger, Sjogren, Nord, & Cedergren, 2019). Furthermore, in another water-limited forest, it has been observed that thinning-induced stem growth and crown area increases are strongly correlated (Sorg, Urech, Mamadzhanov, & Rehnus, 2016). Despite of the higher LAI increase in thinned plots, at the end of this experiment LAI values were still smaller in thinned plots than in control plots, so the duration of the improvement of stem water availability induced by the selective thinning is long. Higher net photosynthetic rates and stem growth in response to thinning in semi-arid habitats may be mediated by higher water availability and stomatal conductance (Moreno-Gutiérrez et al., 2011). These responses were observed in temperate forests only in unusually dry years (Herbs, Mund, Tamrakar, & Knohl, 2015).

This increase in net photosynthetic rate has been associated with an increase in tree growth but also with an increase in the capacity to mitigate climate change due to an increase in forest atmospheric CO<sub>2</sub> uptake. Increased warming and drought, however, will likely alter the capacity of Mediterranean forests to absorb CO<sub>2</sub>, so forest management may be a key factor determining the response of forest C balances to the changing climate (Vayreda, Martínez-Vilalta, Gracia, & Retana, 2012). Mediterranean plants usually close their stomata under severe drought conditions to avoid water loss from transpiration, but stomatal closure also strongly decreases net photosynthetic rates (Mooney, Harrison, & Morrow, 1975; Tenhunen et al., 1980; Llusià & Peñuelas, 2000). Moreover, the emission of volatile organic compounds (VOCs), which are greenhouse gases and contribute to climate change, did not decrease under drought (Llusià & Peñuelas, 2000; Peñuelas et al., 2013), so Mediterranean vegetation can lose the capacity to mitigate climate change under severe drought conditions and can even exacerbate climate change when the effect of both plant respiration and VOC emission exceed atmospheric CO<sub>2</sub> uptake by photosynthesis (Doblas-Miranda et al., 2015; Peñuelas et al., 2013).

Mediterranean ecosystems are currently water limited. Small mitigating interventions could help to preserve their functioning under the impacts posed by increased water stress (Gracia, Vanclay, Daly, Sabaté, & Gyengé, 2011) and the functioning of other interconnected ecosystems (Gasith & Resh, 1999). High stem density could also decrease the water supply for human populations, because vegetation consumes at lot of rainwater (Birot, Gracia, & Palahí, 2011). High stem density could favour the spread of forest fires due to the abundance of dead stems and branches as a consequence of the strong competition for water and resources (Ogaya & Peñuelas, 2007).

In conclusion, our study highlights the appropriateness of selective thinning for improving the growth and conservation of Mediterranean forests, better coping with the

environmental constraints posed by climate change, and increasing the functioning of these ecosystems to mitigate climate change. Selective thinning can also ameliorate several environmental problems typical in Mediterranean areas, such as decreasing the risk and spread of forest fires and increasing the water supply for human populations. 

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#### 350 References

351

- 352 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier,
- 353 M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., González, P., Fensham, R.,
- Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A.,
- 355 & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals
- emerging climate change risks for forests. Forest Ecology and Management, 259, 660-
- 357 684.

358

- Barbeta, A., Ogaya, R., & Peñuelas, J. (2013). Dampening effects of long-term
- 360 experimental drought on growth and mortality rates of a Holm oak forest. Global Change
- 361 Biology, 19, 3133-3144.

362

- Bates, B.C., Kundzewicz, Z.W., Wu, S., & Palutikof, J.P. (2008). Climate Change and
- 364 Water. Technical Paper of the Intergovernmental Panel on Climate Change. Geneva:
- 365 Intergovernmental Panel of Climate Change.

366

- 367 Birot, Y., Gracia, C., & Palahí, M. (2011). Water for forests and people in the
- 368 *Mediterranean region*. European Forest Institute.

369

- 370 Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.D., Allen, C.D., Balice, R.G., Romme,
- W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., & Meyer, C.W.
- 372 (2005). Regional vegetation die-off in response to global-change-type drought.
- 373 Proceedings of the National Academy of Sciences of the USA, 102, 15144-15148.

- 375 Chang, C.T., Sperlich, D., Sabaté, S., Sánchez-Costa, E., Cotillas, M., Espelta, J.M.,
- 376 Gracia, C. (2016). Mitigating the stress of drought on soil respiration by selective
- 377 thinning: contrasting effects of drought on soil respiration of two oak species in a
- 378 Mediterranean forest. *Forests*, 7(263), doi:10.3390/f7110263.

- 380 Cotillas, M., Sabaté, S., Gracia, C., Espelta, J. (2009). Growth response of mixed
- 381 mediterranean oak coppices to rainfall reduction. Could selective thinning have any
- influence on it? Forest Ecology and Management, 258, 1677-1683.

383

- Dai, A.G. (2013). Increasing drought under global warming in observations and models.
- 385 Nature Climate Change, 3, 52-58.

386

- Doblas-Miranda, E., Martínez-Vilalta, J., Lloret, F., Álvarez, A., Ávila, A., Bonet, F.J.,
- 388 Brotons, L., Castro, J., Curiel Yuste, J., Díaz, M., Ferrandis, P., García-Hurtado, E.,
- 389 Iriondo, J.M., Keenan, T.F., Latron, J., Llusià, J., Loepfe, L., Mayol, M., Moré, G., Moya,
- 390 D., Peñuelas, J., Pons, X., Poyatos, R., Sardans, J., Sus, O., Vallejo, V.R., Vayreda, J., &
- 391 Retana, J. (2015). Reassessing global change research priorities in Mediterranean
- 392 terrestrial ecosystems: how far have we come and where do we go from here? Global
- 393 Biology and Biogeography, 24, 25-43.

394

- 395 Fischer, E.M., Schar, C. (2010). Consistent geographical patterns of changes in high-
- impact European heatwayes. *Nature Geoscience* 3, 398-403.

398 Gasith, A., Resh, V. (1999). Streams in Mediterranean climate regions: Abiotic influences 399 and biotic responses to predictable seasonal events. Annual Review of Ecology, Evolution, 400 and Systematics, 30, 51-81. 401 402 Gracia, C., Vanclay, J., Daly, H., Sabaté, S., & Gyengé, J. (2011). Agua para los bosques 403 y la sociedad en el mediterráneo - Un difícil equilibrio. [Water for forests and society in 404 the Mediterranean – A difficult equilibrium]. Barcelona: European Forest Institute. 405 406 Herbs, M., Mund, M., Tamrakar, R., & Knohl, A. (2015). Differences in carbon uptake 407 and water use between a managed and an unmanaged beech forest in central Germany. 408 Forest Ecology and Management, 355, 101-108. 409 Idol, T.W., Morales, R.M., Friday, J.B., & Scowcroft, P.G. (2018). Precommercial release 410 411 thinning of potential Acacia koa crop trees increases stem and crown growth in dense, 8-412 year-old stands in Hawaii. Forest Ecology and Management, 392, 105-114. 413 414 IPCC. (2013). Climate change 2013: The physical Science Basis. Contribution of 415 Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on 416 Climate Change. Cambridge, UK, and New York, NY, USA: Cambridge University Press. 417 418 IPCC. (2018). IPCC 2018: Summary of Policymakers in: Global warming of 1.5°C. An 419 IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of 420

strengthening the global response to the threat of climate change, sustainable

- 422 development, and efforts to eradicate poverty, Masson-Delmotte V. et al. eds, World
- 423 Meteorological Organization, Geneva, Switzerland, 32 pp.

- 425 Jiménez, M.N., Navarro, F.B., Sánchez-Miranda, A., Ripoll, M.A. (2019). Using stem
- 426 diameter variations to detect and quantify growth and relationships with climatic
- variables on a gradient of thinned Aleppo pines. Forest Ecology and Management, 442,
- 428 53-62.

429

- 430 Keyser, T.L. (2010). Thinning and site quality influence aboveground tree carbon stocks
- 431 in yellow-poplar forests of the southern Appalachians. Canadian Journal of Forest
- 432 Research, 40, 659-667.

433

- Liu, D., Ogaya, R., Barbeta, A., Yang X., & Peñuelas, J. (2015). Contrasting impacts of
- continuous moderate drought and episodic severe droughts on the aboveground-biomass
- increase and litterfall of three coexistint Mediterranean Woody species. *Global Change*
- 437 Biology, 21, 4196-4209.

438

- Liu, D., Ogaya, R., Barbeta, A., Yang X., & Peñuelas, J. (2018). Long-term experimental
- drought combined with natural extremes accelerate vegetation shift in a Mediterranean
- holm oak forest. Environmental and Experimental Botany, 151, 1-11.

442

- 443 Lledó, M.J. (1990). Compartimentos y flujos biogeoquímicos en una cuenca de encinar
- 444 del Monte de Poblet. [Biogeochemical compartments and fluxes in a holm oak watershed
- of Poblet Mountains] (Doctoral dissertation). Universitat d'Alacant, Alacant, Spain.

- Lloret, F., Peñuelas, J., & Ogaya, R. (2004). Establishment of co-existing Mediterranean
- tree species under a varying soil moisture regime. Journal of Vegetation Science, 15, 237-
- 449 244.

- Llusià, J., & Peñuelas, J. (2000). Seasonal patterns of terpene content and emission from
- seven Mediterranean woody species in field conditions. *American Journal of Botany*, 87,
- 453 133-140.

454

- 455 López, B., Gracia, C., Sabaté, S., & Keenan, T. (2009). Assessing the resilience of
- 456 Medietrranean holm oaks to disturbances using selective thinning. Acta Oecologica, 35,
- 457 849-854.

458

- 459 Mooney, H.A., Harrison, A., & Morrow, P. (1975). Environmental limitations of
- photosynthesis on a California evergreen shrub. *Oecologia*, 19, 293-301.

461

- 462 Moreno-Gutiérrez, C., Barberà, G.G., Nicolás, E., de Luís, M., Castillo, V.M., Martínez-
- Fernández, F., Querejeta, J.I. (2011). Leaf  $\delta^{18}$ O of remaining trees is affected by thinning
- intensity in a semiarid pine forest. *Plant Cell Environment*, 34, 1009-1019.

465

- Mueller, B., & Seneviratne, S. (2012). Hot days induced by precipitation deficits at the
- 467 global scale. Proceedings of the National Academy of Sciences of the USA, 109, 12398-
- 468 12403.

- 470 Ogaya, R., & Peñuelas, J. (2003). Comparative seasonal gas exchange and chlorophyll
- fluorescence of two dominant woody species in a holm oak forest. Flora, 198, 132-141.

- Ogaya, R., & Peñuelas, J. (2006). Contrasting foliar responses to drought in *Quercus*
- 474 ilex and Phillyrea latifolia. Biologia Plantarum, 50, 373-382.

- 476 Ogaya, R., & Peñuelas, J. (2007). Tree growth, mortality, and above-ground biomass
- accumulation in a holm oak forest under a five-year experimental field drought. *Plant*
- 478 Ecology, 189, 291-299.

479

- 480 Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L.,
- 481 Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W.,
- 482 McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and
- persistent carbon sink in the world's forests. *Science*, 333, 988-993.

484

- Peng, C., Ma, Z., & Lei, X. (2011). A drought-induced pervasive increase in tree mortality
- 486 across Canada's boreal forests. *Nature Climate Change*, DOI: 10.1038/nclimate1293.

487

- 488 Peñuelas, J., Filella, I., Lloret, F., Siscart, D., & Piñol, J. (1998). Comparative field study
- 489 of spring and summer leaf gas exchange and photobiology of the Mediterranean trees
- 490 Quercus ilex and Phillyrea latifolia. Journal of Experimental Botany, 49, 229-238.

491

- 492 Peñuelas, J., Lloret, F., & Montoya, R. (2001). Severe drought effects on Mediterranean
- 493 woody flora in Spain. Forest Science, 47, 214-218.

- 495 Peñuelas, J., Guenther, A., Rapparini, F., Llusià, J., Filella, I., Seco, R., Estiarte, M.,
- 496 Mejía-Chang, M., Ogaya, R., Ibáñez, J., Sardans, J., Castaño, L.M., Turnipseed, A., Duhl,

- T., Harley, P., Vila, J., Estavillo, J.M., Menéndez, S., Facini, O., Baraldi, R., Geron, C.,
- 498 Mak, J., Patton, E.G., Jiang, X., & Greenberg, J. (2013). Intensive measurements of gas,
- water, and energy exchange between vegetation and troposphere during the MONTES
- 500 campaign in a vegetation gradient from short semi-desertic shrublands to tall wet
- temperate forests in the NW Mediterranean Basin. Atmospheric Environment, 75, 348-
- 502 364.

- Peterson, J.A., Seiler, J.R., Nawak, J., Ginn, S.E., & Kreh, R.E. (1997). Growth and
- 505 physiological responses of young loblolly pine stands to thinning. Forest Science, 43,
- 506 529-534.

507

- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I.,
- Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A., Smith,
- 510 P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., & Wattenbach, M. (2013).
- 511 Climate extremes and the carbon cycle. *Nature*, 500, 287-295.

512

- Roberts, S.D., & Harrington, C.A. (2008). Individual tree growth response to variable
- density-thinning in coastal Pacific Northwest forests. Forest Ecology and Management,
- 515 255, 2771-2781.

516

- 517 Sheil, D., Burslem, D.F.R.P., & Alder, D. (1995). The interpretation and misinterpretation
- of mortality rate measurements. *Journal of Ecology*, 83, 331-333.

- 520 Selig, M.F., Seiler, J.R., & Tyree, M.C. (2008). Soil carbon and CO<sub>2</sub> efflux as influenced
- by the thinning of loblolly pine (*Pinus taeda* L.) plantations on the Piedmont of Virginia.

- 522 Forest Science, 54, 58-66.523
- 524 Sorg, J.P., Urech, Z.L., Mamadzhanov, D., & Rehnus, M. (2016). Thinning effects on
- walnut and crown diameter growth and fruiting in the walnut-fruit forests of Kyrgyzstan.
- 526 Journal of Mountain Science, 13, 1558-1566.

- 528 Sullivan, T.P., & Sullivan, D.S. (2016). Acceleration of old-growth structural attributes
- 529 in lodgepole pine forest: Tree growth and stand structure 25 years after thinning. Forest
- *Ecology and Management, 365*, 96-106.

531

- Tang, Z., Chambers, J.L., Guddanti, S., & Barmett, J.P. (1999). Thinning, fertilization,
- and crown position interact to control physiological responses of loblolly pine. Tree
- 534 Physiology, 19, 87-94.

535

- Tang, J., Qi, Y., Xu, M., Misson, L., & Goldstein, A.H. (2005). Forest thinning and soil
- respiration in a ponderosa pine plantation in the Sierra Nevada. Tree Physiology, 25, 57-
- 538 66.

539

- Tenhunen, J.D., Lange, O.L., Braun, M., Meyer, A., Losch, R., & Pereira, J.S. (1980).
- Midday stomatal closure in *Arbutus unedo* leaves in a natural machia and under simulated
- habitat conditions in an environmental chamber. *Oecologia*, 47, 365-367.

- Valinger, E., Sjogren, H., Nord, G, & Cedergren, J. (2019). Effects on stem growth of
- scots pine 33 years after thinning and/or fertilization in northern Sweden. Scandinavian
- 546 Journal of Forest Research, 34, 33-38.

54/	
548	Vayreda, J., Martínez-Vilalta, J., Gracia, M., & Retana, J. (2012). Recent climate changes
549	interact with stand structure and management to determine changes in tree carbon stocks
550	in Spanish forests. Global Change Biology, 18, 1028-1041.
551	
552	Wang, W., Peng, C., Kneeshaw, D.D., Larocque, G.R., and Luo, Z. (2012). Drought-
553	induced tree mortality: ecological consequences, causes, and modeling. Environmental
554	Review 20, 109-121.
555	
556	Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M.,
557	Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook,
558	E.R., Gangodagamage, C., Cai, M., & McDowell, N.G. (2013). Temperature as a potent
559	driver of regional forest drought stress and tree mortality. Nature Climate Change, 3, 292-
560	297.
561	
562	
563	
564	
565	
566	
567	
568	
569	
570	
571	

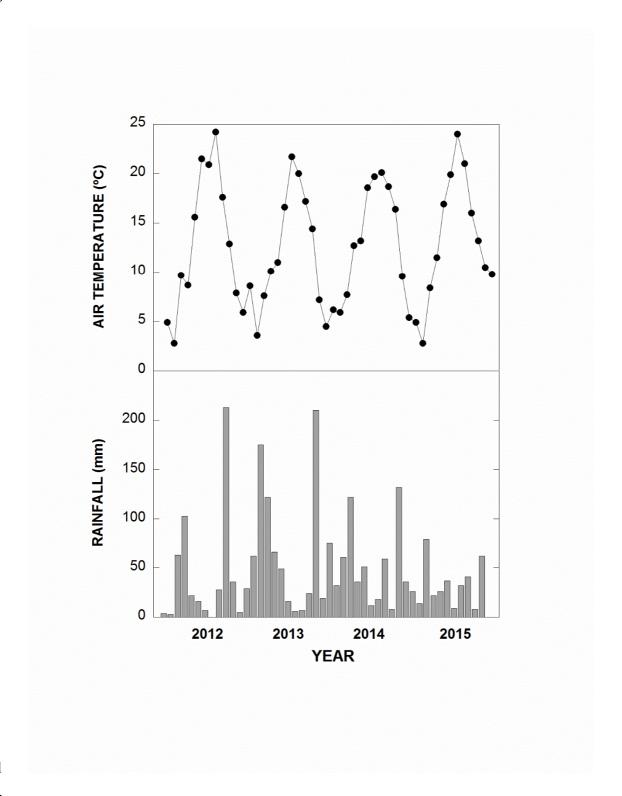
Table 1. Basal area (BA) of the dominant species in each thinned plot immediately before and after thinning.

Plot	Species	BA before thinning	BA after thinning	BA removed (%)
		$(m^2 ha^{-1})$	$(m^2 ha^{-1})$	
1	Q. ilex	43.57	38.41	11.84
	P. latifolia	2.64	1.10	58.39
	A. unedo	10.06	5.80	42.37
	All species	56.27	45.31	19.48
2	Q. ilex	29.31	24.59	16.09
	P. latifolia	2.57	1.77	31.04
	A. unedo	9.75	6.43	34.02
	All species	41.83	33.00	21.11
3	Q. ilex	42.14	33.86	19.64
	P. latifolia	4.94	1.45	70.53
	A. unedo	5.15	3.59	30.36
	All species	53.71	39.53	26.39

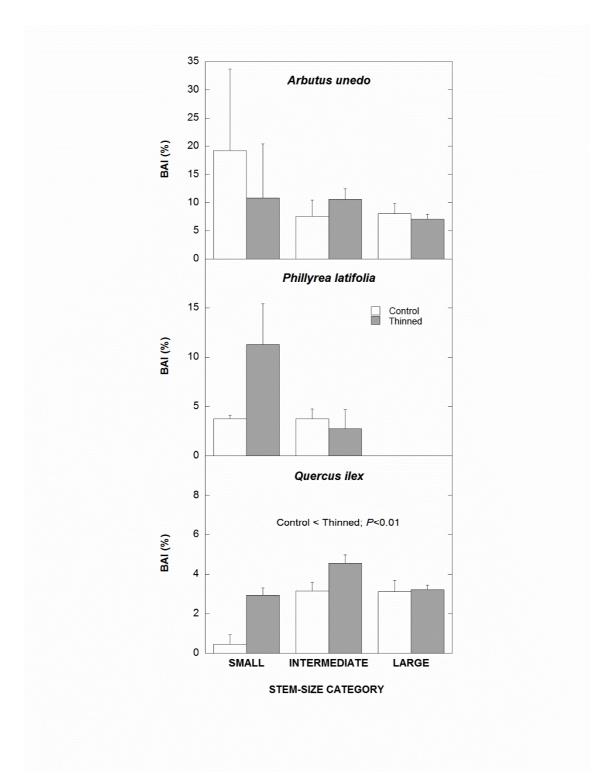
Table 2. Leaf area index (LAI) of the dominant species in each thinned plot immediately before and after thinning.

Plot	Species	LAI before thinning	LAI after thinning	LAI removed (%)
		(m <sup>2</sup> of leaves per m <sup>2</sup>	(m <sup>2</sup> of leaves per m <sup>2</sup>	
		of plot surface)	of plot surface)	
1	Q. ilex	4.52	3.86	14.54
	P. latifolia	0.16	0.07	59.49
	A. unedo	0.77	0.44	43.25
	All species	5.45	4.36	19.95
2	Q. ilex	3.13	2.52	19.49
	P. latifolia	0.18	0.13	28.74
	A. unedo	0.75	0.48	36.55
	All species	4.07	3.14	22.98
3	Q. ilex	4.69	3.54	24.54
	P. latifolia	0.44	0.10	77.54
	A. unedo	0.39	0.30	29.22
	All species	5.64	3.97	29.61

# Figure captions Figure 1. Mean annual temperature and annual precipitation at the study site during the study period. Figure 2. Average percentage basal-area increase (BAI) in the thinned and control plots (3 and 4 plots, respectively) for each species and stem-size category, during the overall studied period. Error bars correspond to the standard error of the mean. Figure 3. Average annual rates of stem mortality in the thinned and control plots (3 and 4 plots, respectively) for each species. Error bars correspond to the standard error of the mean. \*, P<0.05; \*\*, P<0.01. Figure 4. Average increases in aboveground biomass (in percentage and absolute values) in the thinned and control plots (3 and 4 plots, respectively) for each species, during the overall studied period. Error bars correspond to the standard error of the mean. \*, P<0.05; \*\*, *P*<0.01. Figure 5. Average percentage of leaf area index (LAI) increment in the thinned and control plots (3 and 4 plots, respectively) for each species during the overall studied period. Error bars correspond to the standard error of the mean. \*, P<0.05; \*\*, P<0.01.



623 Fig. 1.



629 Fig. 2.

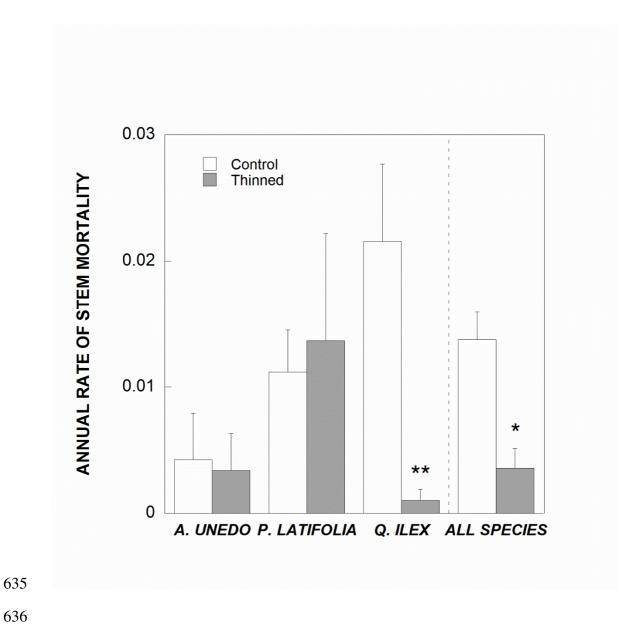
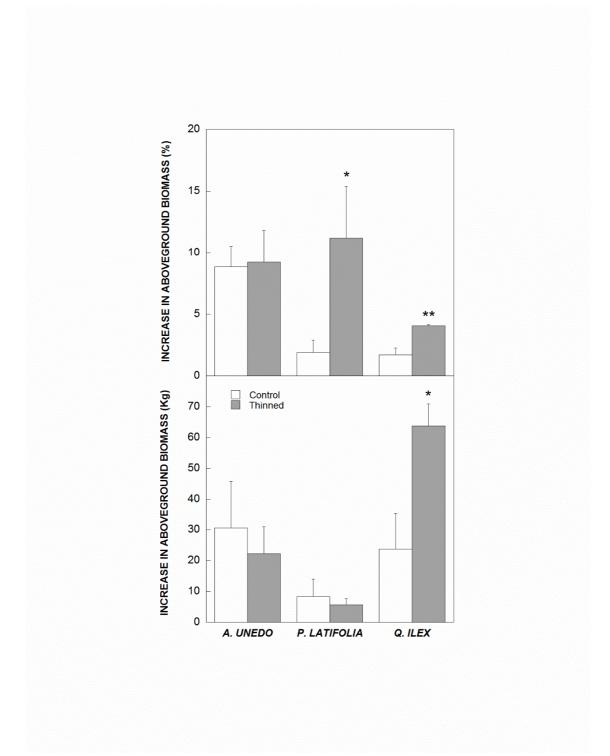


Fig. 3.



645 Fig. 4.

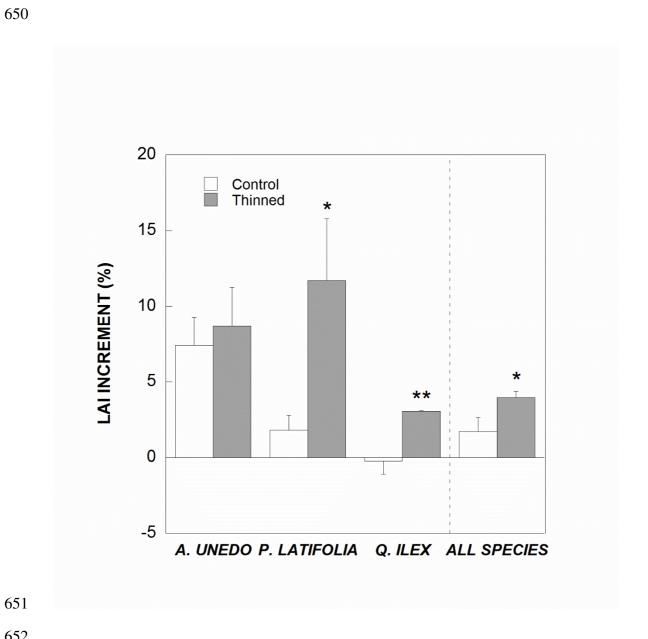


Fig. 5.