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ORIGINAL PAPER

Fall rate of burnt pines across an elevational gradient in a Mediterranean mountain

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Abstract Burnt wood remaining after a wildfire is a biological legacy with important implications for habitat structure, ecosystem regeneration, and post-fire management. Knowledge of the time required for snags to fall is thus a key aspect for planning forest restoration. In this study, we analyze the fall rate of burnt trees in a Mediterranean pine reforestation. Three plots of 18–32 ha were established after a fire across an elevational gradient spanning from 1400 to 2100 m a.s.l., and snag fall rate was measured on a yearly basis using an experimental setup that considered two levels of a thinning treatment: unthinned (where no post-fire management was conducted and all the snags were left standing after the fire) and thinned (where 90% of the trees were cut after the fire and left on the ground). All the snags remained standing during the first and second winter, and thereafter, they collapsed quickly until reaching 100% after 5.5 years. Snags in low-density stands resulting from thinning fell faster than in unthinned stands, but the differences were minor. There was a negative effect of tree diameter on the rate of collapse, especially in the unthinned treatment, but the effect of diameter was minor too. There was no effect of the elevational gradient on fall rate despite patent differences in climatic conditions and pine species across plots. The results support the contention that post-fire fall rate in dense pine plantations in Mediterranean mountains can occur quickly after the second winter and may show little variation across environmental gradients.

Keywords Standing dead trees · Tree fall rate · Burnt wood · Pine plantation · Post-disturbance management · Post-fire dynamics

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Introduction

Wildfire is a common disturbance in many ecosystems of the world (Rowell and Moore 2000; Keeley et al. 2012). After a fire of medium to high intensity, snags—i.e., standing burnt trees—usually remain standing for some time and create a landscape with a complex habitat structure along with downed wood (DeLong et al. 2008; Swanson et al. 2011). This habitat is the starting point for post-fire regeneration, whether natural or assisted. Burnt trees create habitat heterogeneity through their different types, sizes, abundances, and fall or decay rates (Franklin and MacMahon 2000; Lindenmayer et al. 2008). Therefore, they constitute a biological legacy from the past forest that persists during secondary succession whose presence and characteristics may affect successional trajectories and, hence, future community composition (Macdonald 2007; Lindenmayer et al. 2008; Leverkus et al. 2014).

Understanding the rate of tree fall and the causes determining its spatial and temporal patterns is of great interest for several ecological and practical/management reasons. First, burnt trees create habitat heterogeneity which, in turn, may affect key parameters for forest restoration and natural regeneration such as nutrient availability (Marañón-Jiménez et al. 2013), microclimatic conditions (Castro et al. 2011; Marzano et al. 2013), seed dispersal (Rost et al. 2009; Castro et al. 2012; Cavallero et al. 2013), or seed predation and herbivore damage on vegetation (Hebblewhite et al. 2009; Castro 2013; Leverkus et al. 2013). Second, standing burnt trees are an important component of the habitat of numerous species of lichens, bryophytes, mammals, cavity-nesting birds, and several bark- and wood-inhabiting beetles (Bull et al. 1997; Chambers and Mast 2005; Bradbury 2006; Hutto 2006), whose conservation or management requires accurate predictions of the residence time of snags. Third, since fallen wood decomposes faster than standing snags, tree fall rate can affect the decay rate and therefore define the speed of nutrient cycling and the rate of nutrient uptake by plants (Marañón-Jiménez and Castro 2013; Heikkala et al. 2014). Fourth, the amount of burnt biomass and the proportion of standing or downed trees may determine the ease for subsequent management actions such as reforestation, with implications for management costs (Kirby et al. 1998; Leverkus et al. 2012). Finally, standing dead trees may also compromise the safety of recreational or management activities (Wagener 1963; Mitchell and Preisler 1998). In summary, there are many implications resulting from the abundance and condition of burnt wood, and post-fire management requires proper understanding of the timing and potential modifiers of snag collapse.

Snag fall rate has been related to several factors such as decay rate (Aakala et al. 2008), tree species (Mitchell and Preisler 1998; Everett et al. 1999; Heikkala et al. 2014), and silvicultural treatments (Mitchell and Preisler 1998; Huggard 1999; Garber et al. 2005), and nearly all studies have obtained positive relationships between tree diameter and the resistance to collapse (Maser and Trappe 1984; Vanderwel et al. 2006; Parish et al. 2010). However, snag dynamics have mostly been studied in North American coniferous forests (Everett et al. 1999; Boulanger and Sirois 2006; Passovoy and Fulé 2006; Angers et al. 2011; Acker et al. 2013), whereas studies in other biomes and forest types are scant. In addition, there is a lack of studies performed under controlled experimental conditions, in particular including replicated and properly randomized post-fire management regimes. Given the large set of biotic and abiotic variables that may affect snag fall rate, the use of experimental designs is particularly needed in order to draw useful, predictive conclusions for post-fire management.

In this study, we seek to determine the effect of elevation and stand density on the pattern and pace of post-fire snag fall in a burnt Mediterranean pine reforestation. Pines were massively planted in the twentieth century for different purposes, yet scant recent management of these plantations has often resulted in large, dense, and homogeneous stands with a high fire risk (Pausas et al. 2004; Gómez-Aparicio et al. 2009). After the 2005 Lanjarón fire, three experimental plots were created across an elevational gradient spanning ca. 800 m, and stand density was manipulated after the fire through thinning, which created two treatments replicated three times within each elevational level. Burnt trees were thereafter monitored until all had collapsed. Our working hypotheses were that snag fall rate would be affected by a number of factors, namely: (1) the elevational gradient, which generates gradients in parameters that may affect snag residence time such as climatic conditions and pine species; (2) the thinning treatments, because thinning would likely increase susceptibility to wind; and (3) tree size, as larger diameters tend to increase the resistance of snags. Overall, we seek to determine the main factors affecting the residence time of snags in a Mediterranean forest, which underlies their capacity to create structural habitat complexity and represents a relevant consideration for post-fire management decisions.

Methods

Study site and experimental design

The study was conducted in the Sierra Nevada Natural and National Park (SE Spain), in an area that burned in September 2005 (the Lanjarón fire). The fire burned around 1300 ha of 35–45-year-old reforested pine stands on a SW-oriented mountainside. It was a high-intensity crown fire that consumed all the leaves, twigs, and litter and charred the bark of the trunks (Marañón-Jiménez et al. 2013). Terraces occupied all the surface of the study area, and the burnt pines were initially planted on approximately 3-m-wide terrace beds (Leverkus et al. 2012). The pine species were distributed along an elevational/moisture gradient according to their ecological requirements and included *P. pinaster*, *P. nigra*, and *P. sylvestris* (in order of increasing elevation; Table 1). The three species are native in the south of the Iberian Peninsula, yet those of the study area constitute a plantation made in the second half of the twentieth century. Climate in the area is Mediterranean, characterized by precipitation falling mostly during autumn and winter and by a hot, dry summer. Annual precipitation increases with elevation, whereas temperature follows the opposite trend (Table 1). Initial pre-fire pine density differed between plots but was high in all cases (>1000 trees ha^{-1}; Table 1). Snowfall occurs between November and March, persisting up to 3 months above 2000 m a.s.l.

Table 1 Location and characteristics of the study plots

	Plot		
	1	2	3
Coordinates[a]	36°57′12.1″ N 03°29′36.3″ W	36°58′11.9″ N 03°30′1.7″ W	36°58′6.5″ N 03°28′49.1″ W
Elevation (m a.s.l.)[a]	1477	1698	2053
Slope (%)[b]	30.3	28.7	31.4
Plot area (ha)	17.7	23.9	31.7
Subplot area (ha)[c]	2.07 ± 0.20	2.77 ± 0.24	3.86 ± 0.37
Mean daily min. temp. (°C)[d]	6.8 ± 0.2	5.6 ± 0.2	3.4 ± 0.2
Mean daily max. temp. (°C)[d]	17.1 ± 0.2	16.2 ± 0.2	13.4 ± 0.2
Mean ann. precip. (mm)[d]	536 ± 41	550 ± 40	630 ± 42
Soil density (g cm^{-3})[e]	1.25 ± 0.06	1.34 ± 0.07	1.15 ± 0.06
Dominant species	*Pinus pinaster/P. nigra*	*Pinus nigra*	*Pinus sylvestris*
Pre-treatment tree density (individuals ha^{-1})	1477 ± 46	1064 ± 67	1051 ± 42
Tree height (m)	6.3 ± 0.1	6.6 ± 0.1	6.2 ± 0.1
Trunk basal diameter (cm)	21.62 ± 7.2	21.33 ± 5	19.78 ± 6.5

[a] Measured at the centroid of each plot

[b] Average of the slope of the replicates (subplots)

[c] No difference in subplot size across treatments; Kruskal–Wallis test ($\chi^2 = 0.24$; $df = 1$; $P = 0.63$). Values are mean ± 1 SE of the mean

[d] Data obtained from interpolated maps of Sierra Nevada (1981–2010) generated at the Instituto Interuniversitario de Investigación del Sistema Tierra en Andalucía (Granada)

[e] Data from Marañón-Jiménez et al. (2013); for more soil properties refer to the cited article

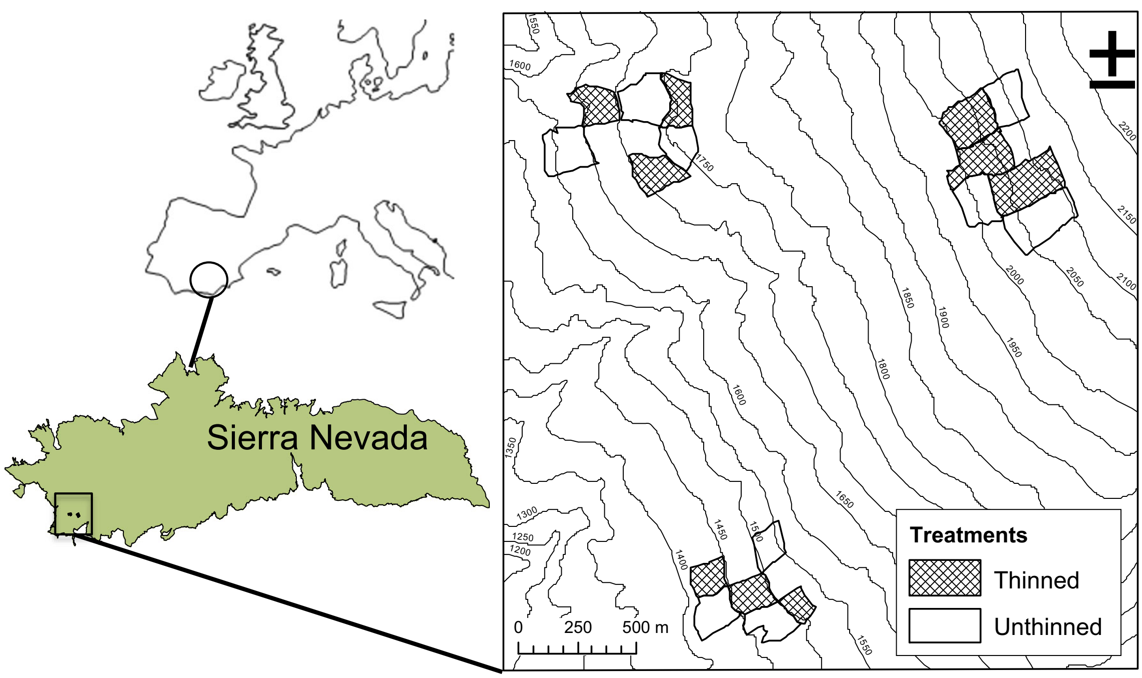

Fig. 1 Map of the study site after the Lanjarón fire in Sierra Nevada (Spain). For further details, see Table 1. The *solid lines* indicate 50 m *contour lines*

Between March and May 2006 (around 7 months after the fire), three plots of 18–32 ha were established at three different elevations (Fig. 1). The plots had a similar orientation, slope, aspect (SW), and soil type (Haplic phaeozems; for details on soils see Marañón-Jiménez et al. 2013), but differed in elevation and related variables such as climate and pine species (Table 1). Within each plot, six subplots were established, which constituted three replicates of two post-fire thinning treatments that differed in the degree of intervention and in final stand density: (1) thinned (T), where ca. 90% of the snags were cut, the main branches were lopped off, the boles were cut in pieces of 2–3 m length, and all the wood was left spread over the ground. The remaining 10% of the snags were left standing with the initial purpose of providing perches for birds, and they were regularly distributed across the whole surface of the subplots (i.e., the forestry staff selected approximately every tenth tree to remain standing). The final density of standing snags depended on the initial tree density, and it ranged between 100 and 140 trees ha^{-1}. (2) Unthinned (U), where all the snags were left standing and no further action was taken. Snag density in this treatment thus represented the initial tree density, and it ranged between 1000 and 1450 trees ha^{-1} (Table 1). Previous to management, tree density did not significantly vary between treatments (Kruskal–Wallis test; $P = 0.29$), nor did tree dbh ($P = 0.78$). The experiment thus consisted of a generalized randomized block design (Quinn and Keough 2002), where the three blocks (plots) were defined by elevation, and each plot contained three replicates (subplots) of each of two thinning treatments. Pine species varied across blocks, which is a normal situation in reforested pine stands across marked elevational gradients. The design thus does not allow separating the contribution of elevation and pine species to the effect of block on fall rate, although the replication within each block allows testing the effects of the other factors within and across elevational levels. All the burnt trees that remained in the area surrounding the study plots were cut and removed (salvage logged).

Snag monitoring

After treatment implementation (between March and May 2006), we randomly selected 100 standing snags per subplot (thus totaling 1800) and tagged them with a metal plaque. We measured snag basal diameter for each of them (averaging two perpendicular measurements made with a large caliper), and snag height for a subset of 20–30 randomly chosen pines per subplot. We monitored the fall rate of the snags between February and March every year until 2011, by when all had collapsed. This corresponds to the 2006–2011 sampling periods hereafter. At each sampling period, we ascribed the state of the snag as standing or fallen. Trees considered fallen could be either totally touching the ground or supported by neighboring snags, but clearly bent in all cases with an angle above 45°. The position at which each snag broke (i.e., from the base of the stump or higher along the trunk) was also noted.

Statistical analyses

All the following analyses were performed in R version 3.1.1 (R Development Core Team 2014).

To test for collinearity between our explanatory variables, we analyzed the effect of thinning (a categorical factor with two levels) and elevation (a categorical factor with three levels) on average snag diameter at subplot level with ANOVA, including both factors and the interaction between them as explanatory variables. Prior to the analysis, the data were log-transformed.

We assessed the effect of the thinning treatment on the proportion of snags that remained standing in each particular year with a Kaplan–Meier survival function. The *survivors* function of the *survival* package (Therneau 2014) estimated the probability that a tree remained standing after each year, and 95% confidence intervals provided a measure of the differences in this probability between the thinning treatments for each consecutive year.

We modeled snag retention time with linear mixed-effects models. We first developed a full model, specifying thinning, elevation, and snag basal diameter, as well as all the possible interactions between these factors, as fixed effects. As a random effect, we specified subplot (a categorical factor with 18 levels). To determine the significance of the terms included in the full model, we used stepwise elimination and likelihood ratio tests (Pinheiro and Bates 2000; Crawley 2013). The significance of a term was considered at $\alpha = 0.05$, and data were square root-transformed prior to analysis. As the range of available snag diameters differed across the two thinning treatments (see Results), for this analysis we considered only those snags whose diameter fell within the range of diameters available in both treatments (i.e., from 12.7 to 33.7 cm). This resulted in the use of 778 and 840 snags in the unthinned and thinned treatments, respectively, in the statistical procedures (see Online Resource 1 for the number of individuals per replicate). The same modeling procedure was also performed for the snags of each plot separately (Online Resource 2). Mixed-effects models were performed with the *lme* function from the *nlme* package (Pinheiro et al. 2014).

Results

Snag basal diameter across elevations and thinning treatments

Snag diameter differed significantly between elevations ($\chi^2 = 29.5$; $df = 2$; $P < 0.01$), with an overall value of 21.66 ± 7.24 cm for Plot 1, 21.33 ± 5.08 cm for Plot 2, and 19.78 ± 6.6 cm for Plot 3 (values are mean $\pm$ 1 SE of the mean throughout the paper). Snag diameter also differed between treatments ($\chi^2 = 695.9$; $df = 1$; $P < 0.001$), with an average of 17.73 ± 4.75 cm in the unthinned treatment and 24.12 ± 6.28 cm in the thinned treatment. However, the effect of thinning varied across plots, which gave rise to a significant elevation x thinning interaction ($\chi^2 = 23.6$; $df = 2$; $P < 0.001$; Fig. 2). Thinning had an effect size of 1.45 in Plots 1 and 3, whereas in Plot 2 the diameters of trees in the thinned treatment were only 1.20 times as large as in the unthinned treatment. Thus, although the effect sizes differed, the direction of the thinning effect was still the same regardless of the plot. The differences in diameter between treatments were likely the result of decisions of workers, who non-randomly selected smaller trunks for cutting in the thinned treatment (despite cutting more or less every tenth snag in a regular pattern). As this outcome generated collinearity between the thinning treatment and snag diameter, below we express the results of snag fall rate with consideration of this issue and avoiding the provision of average effects of the thinning treatment.

Snag fall rate

The cumulative proportion of collapsed snags averaged 0% in 2006 and 2007, 13.3% in 2008, 84.6% in 2009, 98.2% in 2010, and 100% by the end of the study period in 2011 (thus 5.5 years after the fire). There were significant differences between treatments in these proportions in 2008 and 2009 according to the Kaplan–Meier model (Fig. 3), although the differences were small and this model did not consider the effect of snag diameter (see below). The largest number of snags collapsed between the 2008 and 2009 assessments (Fig. 3). Overall, trees broke off at the stump in 98% of the cases (for a photograph see Online Resource 3), whereas 2% of the snags were broken at a higher position of the trunk.

The mixed-effects model showed significant main effects of elevation and thinning (Table 2): Average snag retention time was higher in Plot 2 (676.6 ± 41.9 days) than in either Plot 1 (577.7 ± 9.8 days) or Plot 3 (597.4 ± 36.2 days), and it was also greater in unthinned than in thinned plots (Fig. 4). Snag basal diameter had an overall positive effect on retention time, but this effect was modulated by interactions with elevation and thinning (Table 2). While the diameter effect was pronounced in the unthinned treatment, it was close to inexistent in the thinned treatment (Fig. 4). Similarly, the model coefficients for the slope of the diameter effect were greater for Plot 2 (0.51) than for either Plot 1 (0.31) or Plot 3 (0.26). Similar effects of thinning and diameter occurred within each plot (Online Resource 2).

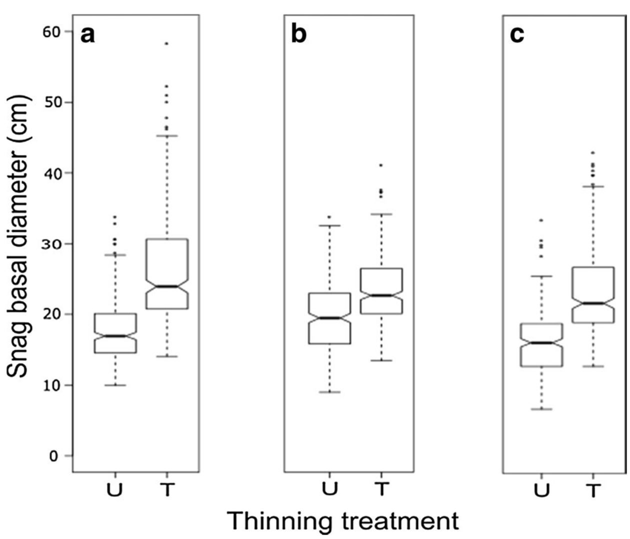

Fig. 2 Snag basal diameter across the two post-fire thinning treatments: Unthinned (U) and thinned (T), and across elevations, after the Lanjarón wildfire: **a** Plot 1, **b** Plot 2, **c** Plot 3. The *lines in bold* represent medians, and the *boxes* indicate the first and third quartiles of the data. Whiskers are either the minimum/maximum values or 1.5 times the interquartile range of the data, in which case outliers are shown as points

Discussion

In this study, the burnt pines of a Mediterranean reforestation fell quickly, with most of the snags having collapsed 3.5 years after the fire. Snags with larger diameter remained standing for longer at sites with high snag densities, and snags at sites with low densities due to post-fire thinning collapsed faster irrespective of their size. However, these effects were small, and 100% of the snags had collapsed 5.5 years after the fire. Our results provide

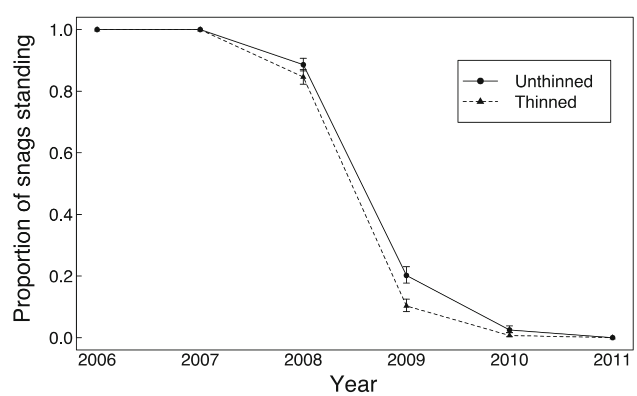

Fig. 3 Fall rate of the snags according to the Kaplan–Meier model across years and thinning treatments. *Error bars* indicate the 95% confidence interval of the proportion of snags standing each year, and significant effects of thinning arose in years for which the bars do not overlap

Table 2 Effects of snag diameter, the thinning treatment, and elevation on snag retention time as estimated with linear mixed models

Terms excluded from the model			Terms kept in the model			
Term	L. ratio	*P* value	Term	*df*	*F*	*P* value
Diameter × thinning × elevation	0.95	0.62	Diameter	1, 1596	65.84	<0.001
Thinning × elevation	3.64	0.16	Thinning	1, 14	8.66	<0.05
			Elevation	2, 14	4.48	<0.05
			Diameter × thinning	1, 1596	33.72	<0.001
			Diameter × elevation	2, 1596	10.40	<0.001

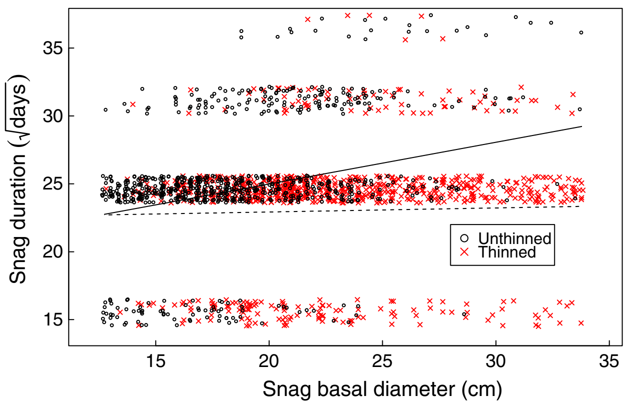

Fig. 4 Effects of snag diameter on snag duration for each of the thinning treatments. The lines are best-fit lines from the linear mixed-effects model: The *solid line* is for the unthinned treatment, while the *dashed line* is for the thinned treatment. The points are jittered on both axes to reduce overlapping

insights for the post-fire management of Mediterranean pine stands, with the advantage of having used a carefully designed experimental approach.

Tree fall after the Lanjarón fire was quite fast compared to other studies (Harrington 1996; Chambers and Mast 2005; Russell et al. 2006; Ritchie et al. 2013), and we attribute this to several mutually non-exclusive factors. First, the cause of mortality, fire, generally makes snags less persistent and more susceptible to wind when compared to other disturbances such as insect outbreaks (Morrison and Raphael 1993). Second, high pre-fire stand densities led to a high fire intensity and severity, which may have accelerated fall rates due to the quick death of the trees (Ritchie et al. 2013). Third, *Pinus* species generally show short snag fall times as compared to other species such as *Abies spp*. (Landram et al. 2002; Ritchie et al. 2013). And fourth, the study plots were located on an exposed mountain slope with strong winds occurring in pulses during the autumn and winter that likely accelerated the collapse of the snags (see below).

Although our results showed little effect of the analyzed factors on fall rate, some patterns did emerge. First, greater snag diameter increased retention time, which is consistent with the general findings reported in other studies (Dahms 1949; Morrison and Raphael 1993; Mitchell and Preisler 1998; Russell et al. 2006). This positive effect of the diameter on snag persistence may be related to the greater stability provided by the higher proportion of heartwood as compared to sapwood in larger trees, which provides greater resistance to decay (Russell et al. 2006; Smith et al. 2009). Additionally, smaller snags tend to be rapidly colonized by decay fungi (Vanderwel et al. 2006), resulting in a loss of bole strength with increased likelihood of falling (Harrington 1996). While the magnitude of the snag diameter effect on fall rates was small in this study, it would likely be amplified in cases with a more heterogeneous forest age structure, as our study only encompassed snags with base diameters of 12.7–33.7 cm.

As a second pattern, the thinning treatment affected the rate at which snags collapsed and also modulated the effect of snag diameter, likely due to the effect of thinning on snag density. In general, snags within areas of higher snag density (i.e., in the unthinned treatment) remained standing for longer than in the low-density thinned treatment. Similar results of longer snag retention time in denser stands have been reported previously (e.g., Mitchell and Preisler 1998; Russell and Weiskittel 2012) and likely appear because higher snag densities act as wind shields that delay the collapse of snags located away from the border of the stand (Vanderwel et al. 2006). This is further supported by the fact that the effect of trunk basal diameter on snag duration, although positive for both thinning treatments, was much weaker in thinned subplots: In a situation where there was no protection provided by neighboring snags, the resistance conferred by larger snag diameter diminished. In fact, maximum peak wind speed registered in 2010 at our study area, measured in a micrometeorological station at 2200 m a.s.l., reached 17.7 m s^{-1} within the unthinned treatment and 37.6 m s^{-1} in the surrounding salvage-logged matrix (P. Serrano-Ortiz, pers. comm.), so that the dense stands buffered the strength of peak windy events (Chambers and Mast 2005; Edworthy et al. 2012).

Finally, we found only small effects of elevation on fall rate despite the variation in climatic conditions and species across plots. We had hypothesized higher fall rates at higher elevation due to differences in rainfall, snow load, and wind speed. However, the slightly greater snag retention time in Plot 2 than in the other plots (ca. 100 days) and the greater effect of the thinning treatment on retention time in Plot 2 do not correspond to any clear elevational trend. Indeed, if any elevation-related effects existed, they may either have been offset by the quick fall of the snags, or canceled-out by counteracting effects, as more than one factor varied across the plots. For example, factors such as the different wood density and concentration of lignin in the heartwood of the different pine species (De Aza et al. 2011) may have resulted in different decay rates across plots. Further, Mitchell and Preisler (1998) proposed that the effects of lower decay rate resulting from lower temperature might counteract those of higher wind speed and snow load at higher elevation. Further studies controlling factors such as species are required to assess the effect of elevation on snag fall rate, but a key point here is that tree species (pines in our case) generally change across sharp elevational gradients, so that maintaining this factor constant is often impossible and, in any case, does not correspond to most real-world scenarios. Thus, our results provide strong support from a management point of view to assume that fall rate in dense pine stands may be similar across elevational gradients, irrespective of the underlying mechanisms that drive the collapse of snags.

In conclusion, our results show that the collapse of the snags of a burnt pine reforestation in a Mediterranean mountain was fast and little affected by snag density, size, or elevational location. Although differences related to climatic and species-specific characteristics might be expected, it is likely that counteracting factors, together with the overall short time required for snag fall, eliminated potential differences across elevations. This suggests that land managers may have consistent predictions related to snag fall rate after fire in pine reforestations and thus may plan activities accordingly. From an ecological perspective, burnt wood, whether standing or after its collapse, is a biological legacy with important implications for ecosystem structure and functioning. Dead wood provides habitat and/or resources for a wide set of taxa of lichens, fungi, plants, and animals (Lindenmayer et al. 2008; Thorn et al. 2016; Rost and Pons 2017), and it promotes plant natural regeneration through the enhancement of soil fertility and the increase in the spatial and temporal heterogeneity in the microhabitat conditions that affect plant recruitment (Macdonald 2007; Marañón-Jiménez and Castro 2013; Moya et al. 2015; Leverkus et al. 2014, 2016). Local forest services may seek to remove the burnt wood in order to facilitate reforestation in areas with low potential for natural regeneration, to prevent visitor accidents caused by falling trunks near roads and trails, or for other management targets. However, given the fast rate of snag collapse observed in this study and the generally observed positive role of burnt wood on natural regeneration, we propose that policies of total or partial snag retention be implemented in the post-fire management of Mediterranean pine forests.

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