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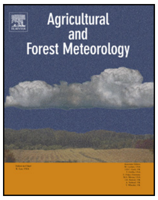

Past logging, drought and pathogens interact and contribute to forest dieback

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ABSTRACT

Forest dieback is one of the most widespread responses to global-change drivers, such as climate warming-related drought stress and the spread of pathogens. Although both climatic and biotic stressors have been studied separately, much less is known on how drought and pathogens interact and induce dieback, particularly in formerly used forests. We determine the roles played by each of those drivers as factors causing recent dieback in three Pyrenean silver fir stands: a managed site subjected to past logging and two unmanaged sites not logged for the past 50 years. The age, size, recent competition, and basal-area increment (BAI) trends of non-declining and declining trees, and the presence of fungal pathogens were investigated. Growth patterns at yearly to decadal time scales were compared to distinguish the roles and interactions played by the different stressors. In the managed site, declining trees displayed low growth already before logging (1950–1970s). In both unmanaged sites, declining and non-declining trees displayed divergent growth patterns after extreme droughts, indicating that dieback was triggered by severe water deficit. We did not find indications that fungal pathogens are the primary drivers of dieback, since a low proportion of declining trees were infested by primary pathogens (10%). However, trees with the primary fungal pathogen *Heterobasidion* showed lower BAI than non-declining trees. On the other hand, the secondary fungal pathogen *Amylostereum* was isolated from a higher number of trees than expected by chance. These findings highlight the importance of legacies, such as the past use in driving recent forest dieback. Past forest use could predispose to dieback by selecting slow-growing trees and thus, making some them more vulnerable to drought and fungal pathogens.

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1. Introduction

Global-change drivers, such as climate warming and aridification, land-use modifications and biotic agents, alter the structure, dynamics, services, and functioning of forests (Bonan, 2008). Forest dieback and the consequent massive tree mortality events are becoming prominent responses to those drivers, questioning the ability of many forests to act as carbon sinks (Dobbertin et al., 2007; Allen et al., 2010). Therefore, understanding and modelling the roles and interactions played by these drivers, which act at different temporal and spatial (region, stand, and tree) scales, are challenging ecologists who are trying to determine the cause–effect relationships and their relative importance (McDowell et al., 2013).

Climatic stressors, such as droughts are probably the best-characterized causes of forest dieback in diverse biomes around the world (see Bigler et al., 2006, 2007; Adams et al., 2009; Van Mantgem et al., 2009; Williams et al., 2013; Cailleret et al., 2014; Zhang et al., 2014). Most authors have treated separately drought-induced and pathogen-driven forest mortality cases, but this division is arbitrary since pathogens usually attack trees already stressed by drought (McDowell et al., 2013). Therefore, to understand how dieback proceeds, we must consider how all potential dieback factors (drought, biotic agents) interact and if they are related to past forest modifications by humans (such as structure changes or fires). Fungal pathogens are one of the most important drivers in the final phase of drought-induced mortality (Oliva et al., 2014); however, despite its importance, little is known about fungal diseases with regard to quantified

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Table 1
Characteristics of the three silver fir sites. Non-declining and declining trees were defined as those with more than or less than or equal to 50% crown cover, respectively.

Site (code)	Latitude (N)	Longitude (W)	Aspect	Elevation (m.a.s.l.)	Slope (°)	Basal area ($m^2\ ha^{-1}$)	No. trees	Percentage of non-declining/declining trees
Cotatuero (CO)	42°39′06″	0°02′36″	S–SW	1450	34	29.4	59	44/56
Turieto (TU)	42°38′51″	0°04′47″	N	1470	37	29.7	38	58/42
Paco Ezpela (PE)	42°44′25″	0°49′33″	N–NE	1170	27	15.1	45	36/64

information, spatial–temporal effects or their relationship with other stressors. First, it has been postulated that climate warming will increase the impact of pathogens on forests; however, the abundance of those biotic stressors may also depend on changes in the forest structure (e.g., past thinning) (Oliva et al., 2009; Oliva and Colinas, 2010), which determine recent tree-to-tree competition (Ayres and Lombardero, 2000). For instance, past thinning creates stumps, which act as expansion foci for several root-rot fungi, thus making trees more vulnerable to drought by reducing their vigor and growth (Oliva et al., 2014). Second, in Europe the abandonment of traditional forest use and changing conservation policies have contributed to the increase in tree density and cover, leading to increased competition between trees. Such densification could increase the competition for water between neighbouring trees in mesic sites during dry periods or in drought-prone areas, predisposing trees to dieback (Linares et al., 2010). Third, it is expected that pathogens may interact with drought stress, potentially leading to non-linear (threshold-type) responses in tree vigor and growth, which will require new analytical approaches (Camarero et al., 2015). Fourth, little is known about the involvement of pathogens in long-term dieback processes. For example, Manion (1991) considered fungal pathogens as opportunistic factors affecting previously stressed trees; however, pathogens could also act as primary drivers of dieback (Oliva et al., 2014). Last but not least, one should consider the role played by selective cuttings in changing the structure of the stand. Selective cuttings mainly remove the largest trees, leaving some big trees to produce seeds and smaller trees to provide protection to the incoming regeneration. It has been hypothesized that dieback mainly affects less-vigorous trees that are unable to adapt to the new conditions of the stand that are created as a result of the cuttings (Oliva and Colinas, 2007). To address these issues and to forecast how vulnerable forests will be to new climatic and land-use scenarios, we must improve our knowledge of dieback processes by integrating and analyzing the roles played by these less-studied factors.

In this study, we carried out a comprehensive assessment of forest dieback causes (climate and drought stresses, competition and fungal pathogens) in three silver fir (*Abies alba*) Pyrenean stands: one managed site that had been subjected to changes in forest structure in the past and two unmanaged sites located within a National Park where no logging had occurred for the past 50 years. Silver fir dieback has been an ongoing process in the western Pyrenees since 1980s (Camarero et al., 2011). Previous studies have evaluated different drivers involved in the silver fir dieback events and mostly focused either on the roles played by droughts (Linares and Camarero, 2012a,b) or by fungal pathogens (Oliva and Colinas, 2007). However, in this study, we performed a multifactorial assessment of potential drivers of silver fir dieback and their interactions with forest structure. We used new techniques that enabled comparing the past radial growth of declining and non-declining silver fir trees showing different levels of defoliation, here used as a proxy of vigor. Specifically, (i) we reconstructed and analyzed the growth patterns and trends and their responses to climate in declining and non-declining silver fir trees; (ii) we then related those growth patterns to several factors to determine their roles as drivers of dieback. We hypothesized that drought triggers dieback (inciting factor sensu Manion, 1991), whereas past-use predisposes trees to decline and fungal pathogens contribute to final tree death. In particular, we expected that: trees with more severe defoliation and recently dead trees would show the lowest growth rates, their growth patterns would be most sensitive to drought, they would be subjected to the highest competition levels and that fungal pathogens would be detected frequently in their wood. Since climate models forecast warmer and drier conditions, dieback processes could become more widespread, affecting temperate forests, such as Pyrenean silver fir stands. This study aims to improve the knowledge on the roles played by dieback agents so as to evaluate the vulnerability of the silver fir populations and similar temperate conifer forests.

2. Material and methods

2.1. Study sites

The three study sites were located in northern Aragón in the central-western Spanish Pyrenees (Fig. 1, Table 1). The sites are three silver fir (*A. alba* Mill.) stands located near the south-western limit of the distribution of the species. Here, silver fir usually grows in mesic sites on north-facing slopes, forming pure or mixed forests with European beech (*Fagus sylvatica* L.) or Scots pine (*Pinus sylvestris* L.). All stands were situated on deep and basic soils and formed mixed forests. The understory vegetation was dominated by European box (*Buxus sempervirens* L.). Three silver fir stands characterized by abundant dominant trees with high levels of defoliation were selected (Table 2). Given that we were interested in comparing silver fir stands with diverse historical management,

Table 2
Features of the non-declining (>50% crown cover) and declining silver fir trees (≤50% crown cover) at the three study sites. Different letters show significant differences ($P < 0.05$) between non-declining and declining trees for each variable (Mann–Whitney tests). Values are means ± SE.

Site (code)	Tree type	No. trees (no. radii)	dbh (cm)	Basal area increment ($cm^2\ year^{-1}$) for the period 2002–2012	Age (years)	Crown cover (%)	No. trees used to calculate the competition index	Competition index
Cotatuero (CO)	Non-declining	26 (49)	44.8 ± 3.4	14.3 ± 1.7b	115 ± 4	96.1 ± 1.8b	17	2.86 ± 0.58
	Declining	33 (57)	45.3 ± 1.9	8.3 ± 1.0a	115 ± 11	16.8 ± 3.2a	15	1.90 ± 0.25
Turieto (TU)	Non-declining	22 (43)	34.2 ± 2.2	14.5 ± 1.6b	84 ± 4	98.2 ± 1.2b	16	4.40 ± 0.66
	Declining	16 (31)	38.5 ± 2.0	6.7 ± 0.7a	88 ± 3	17.8 ± 3.3a	8	4.86 ± 0.97
PacoEzpela (PE)	Non-declining	16 (30)	40.3 ± 1.8b	21.6 ± 2.4b	90 ± 4	86.6 ± 2.6b	10	2.53 ± 0.76
	Declining	29 (52)	34.2 ± 1.2a	8.2 ± 0.7a	92 ± 3	19.3 ± 3.8a	16	1.76 ± 0.24

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