Strong resilience of soil respiration components to drought-induced die-off resulting in forest secondary succession

Josep Barba1,2 · Jorge Curiel Yuste3 · Rafael Poyatos1 · Ivan A. Janssens4 · Francisco Lloret1,2

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Abstract How forests cope with drought-induced perturbations and how the dependence of soil respiration on environmental and biological drivers is affected in a warming and drying context are becoming key questions. The aims of this study were to determine whether drought-induced die-off and forest succession were reflected in soil respiration and its components and to determine the influence of climate on the soil respiration components. We used the mesh exclusion method to study seasonal variations in soil respiration (\(R_S\)) and its components: heterotrophic (\(R_H\)) and autotrophic (\(R_A\)) [further split into fine root (\(R_R\)) and mycorrhizal respiration (\(R_M\))] in a mixed Mediterranean forest where Scots pine (\(Pinus sylvestris\) L.) is undergoing a drought-induced die-off and is being replaced by holm oak (\(Quercus ilex\) L.). Drought-induced pine die-off was not reflected in \(R_S\) nor in its components, which denotes a high functional resilience of the plant and soil system to pine die-off. However, the succession from Scots pine to holm oak resulted in a reduction of \(R_H\) and thus in an important decrease of total respiration (\(R_S\) was 36 % lower in holm oaks than in non-defoliated pines). Furthermore, \(R_S\) and all its components were strongly regulated by soil water content-and-temperature interaction. Since Scots pine die-off and \(Quercus\) species colonization seems to be widely occurring at the driest limit of the Scots pine distribution, the functional resilience of the soil system over die-off and the decrease of \(R_S\) from Scots pine to holm oak could have direct consequences for the C balance of these ecosystems.

Keywords Heterotrophic respiration · Autotrophic respiration · Partitioning fluxes · Mediterranean forest · \(Pinus sylvestris\)

Introduction

Drought-induced forest die-off episodes are being increasingly reported globally (Allen et al. 2010), raising concerns regards their possible association with recent global warming, at least in some parts of the world (Carnicer et al. 2011). Increased tree defoliation and mortality rates have been related to chronic and episodic drought in the Mediterranean region (Peñuelas et al. 2001; Carnicer et al. 2011), where the projected increase in the frequency and intensity of droughts (Stocker et al. 2013) may enhance the risk of extensive forest die-off. Widespread drought-induced tree mortality can have dramatic effects on forest C cycling (Reichstein et al. 2013) which may differ from...
those reported for other disturbances such as fire or pest outbreaks (Anderegg et al. 2013; Borkhhuu et al. 2015). Forest ecosystems store over two-thirds of the C in their soils (Dixon et al. 1994), but the impact of drought-induced tree mortality on soil C fluxes and their post-disturbance dynamics remains poorly understood (Allen et al. 2015).

The trajectory of ecosystem C cycling in stands where the dominant overstorey species has been severely affected by a die-off event is complex in space and time (Edburg et al. 2012; Reed et al. 2014; Borkhhuu et al. 2015). At sub-decadal timescales, the trend in forest C uptake largely depends on disturbance intensity and the degree of overstorey canopy loss, the spatial pattern of tree dieback (i.e. clustered, diffuse), the compensatory responses by surviving dominant trees, and the response of understorey vegetation to competition release (Amiro et al. 2010; Brown et al. 2010; Gough et al. 2013). With regard to forest soil C losses, die-off episodes immediately curtail root and mycorrhizal respiration and reduce exudate supply from roots to soil, but they also stimulate decomposition of litter, roots and dead wood (Nave et al. 2011). Moreover, die-off episodes may increase soil moisture (Redding et al. 2008), which could enhance soil organic matter decomposition rates in water-limited ecosystems. Nevertheless, our knowledge on post-dieback ecosystem (and soil) C fluxes is still incomplete, because (1) it largely arises from studies where pests or wildfires, not drought, were the main disturbance drivers, and (2) it lacks a detailed understanding of the post-dieback trajectories of soil respiration components [heterotrophic respiration (R_h), autotrophic respiration (R_A), fine root respiration (R_fk), mycorrhizal respiration (R_M)] and their responses to environmental drivers.

Drought-induced tree mortality episodes often result in a complex spatial pattern of standing dead trees and partially defoliated individuals, together with apparently unaffected trees. These episodes may cause vegetation shifts within years or decades if adult mortality and recruitment of the dominant and most affected species are not balanced through time (Lloret et al. 2012). Given that the substituting species will likely be more drought resistant, such species replacement could have persistent effects on both stand C uptake and release processes. The spatial distribution of soil CO_2 effluxes under non-limiting soil moisture conditions is sensitive to local changes in vegetation composition following tree mortality (Barba et al. 2013), but we do not know whether the response of soil CO_2 effluxes to the main abiotic drivers (i.e. soil temperature and moisture) differs along the stages of an ongoing vegetation shift. In Mediterranean forests, the seasonal correlation between plant productivity and the course of moisture and temperature hinders determination of the effect of these variables on R_S (Tedeschi et al. 2006) because of the inherent seasonal variability of plant photosynthetic activity and belowground C allocation (Reichstein et al. 2002; Keenan et al. 2009).

The variability of soil CO_2 efflux associated with the environmental drivers may also be mediated by the differential metabolic response of microbes, roots and rhizosphere to moisture and temperature changes (Uren 2000; Kuzyakov 2006; Moyano et al. 2010). Changes in microbial community composition have been observed following drought-induced forest die-off and succession (Curiel Yuste et al. 2012), but how these shifts in microbial community composition modify the contribution of autotrophic and heterotrophic respiration to total soil respiration remains poorly understood.

Drought-induced dieback episodes, characterised by increased crown defoliation and mortality rates, have been reported in several Scots pine (Pinus sylvestris L.) populations in the northeast Iberian Peninsula (Martínez-Vilalta and Piñol 2002; Galiano et al. 2010; Hereš et al. 2012). In particular, extreme drought events together with a lack of forest management caused several Scots pine die-off episodes at the Prades Mountains in the 1990s and 2000s (Martínez-Vilalta and Piñol 2002; Hereš et al. 2012) and the associated holm oak (Quercus ilex L.) colonisation (Vilà-Cabrera et al. 2013). These processes have resulted in important changes not only in aboveground components of the forest (Aguadé et al. 2015) but also in the belowground part, altering soil microbial diversity and structure (Curiel Yuste et al. 2012), litter decomposition and nutrient cycling (Barba et al. 2015) and spatial variability of soil respiration (Barba et al. 2013). In this study, we aim to quantify the effects of this Scots pine drought-related die-off and the consequent holm oak colonisation on soil respiration and its components, at seasonal and annual timescales. During 1 year, we measured the seasonal variation of soil respiration and its heterotrophic and autotrophic (roots and mycorrhiza) components, associated with the different stages of this drought-induced die-off and species-replacement process: non-defoliated pines (NDP), partially defoliated pines (DFP), dead pines (DP), and holm oaks (HO).

We hypothesized that:

1. Heterotrophic respiration would show a gradual increase across this die-off gradient (from NDP to DFP and DP) and autotrophic respiration would decrease because of reduced above- and belowground plant activity in DFP and DP.
2. Given that holm oak is a more drought-tolerant species compared to Scots pine, for this drought-exposed site we expected higher soil respiration in holm oak and lower sensitivity to decreasing soil moisture during summer drought compared to Scots pine.
3a. The spatial and temporal variation in heterotrophic soil respiration would be mainly dependent on environmental variables (soil temperature and moisture), whereas these variables would explain little variability for autotrophic respiration.

3b. Since vegetation has the capacity to modify soil environmental conditions, we also hypothesized that the vegetation die-off and the ongoing species succession would largely influence soil CO₂ effluxes via modifications in environmental conditions such as soil water content (SWC).

Materials and methods

Study site

The study was conducted in a mixed forest in the Titllar Valley (Prades Mountains, northeastern Iberian Peninsula). The climate is Mediterranean, with a mean annual temperature of 11.2 °C and precipitation of 664 mm (Ninyerola et al. 2007a, b). The experimental area was located on the northwest face of the valley at an elevation between 1010 and 1030 m a.s.l. with a steep slope (33°). Soils are Xerochrepts with a clay loam texture (49 % sand, 32 % silt, 19 % clay) and a relatively high gravel content of 46 % (Barba et al. 2013; Sus et al. 2014). The substrate consists of fractured metamorphic schist that outcrops on a large part of the study area. Mineral soil is slightly acidic (pH is 6.2) and contains 5.9 % C, 0.27 % N and 0.044 % P (Curiel Yuste, unpublished results). No differences are found in C, N or P availabil- ity or in soil C pools (both quality and quantity) between soils associated with the different type of trees (Curiel Yuste et al. 2012). For more information related to the study area, see Hereter and Sánchez (1999); Barba et al. (2013).

This mixed forest is mainly dominated by Scots pine (Pinus sylvestris L.) in the overstorey and holm oak (Quercus ilex L.) in the understorey, with total stem density of 2235 stems ha⁻¹ (Poyatos et al. 2013). Severe drought events since the 1990s (Martínez-Vilalta and Piñol 2002) and particularly in 2001–2003 and 2005–2008 (Hereş et al. 2012) have affected the Scots pine populations, inducing a mean crown defoliation of 52 % and standing mortality of 12 % (Vilà-Cabrera et al. 2013). This situation, coupled to the low regeneration of pines (Vilà-Cabrera et al. 2013) is currently driving the replacement of pines by oaks as the dominant overstorey species.

Experimental design

Experiment scheme

Soil respiration fluxes were measured close to 12 trees (less than 2 m from the tree stem) belonging to the different stages along the vegetation shift following the Scots pine die-off process (henceforth, type of tree): three NDP, three DFP, three DP and three HO. The maximum distance between measuring points was ca. 200 m. DP were devoid of needles and small branchlets, and only the main bole and primary branches were still standing. Hereş et al. (2012) found that 86 % of the standing mortality resulted from the drought events in 2001–2003 and 2005–2008. Therefore we estimate that these trees have been dead for 3–11 years. The degree of pine defoliation was visually estimated as the percentage of green needles relative to a non-defoliated canopy of a similar sized tree from the same population (Galiano et al. 2010). Defoliated pines had less than 50 % of green leaves. Diameter at breast height for each type of tree was 37 ± 7 cm in NDP, 59 ± 9 cm in DFP, 58 ± 7 cm in DP and 14 ± 8 cm in HO (mean ± SD). The Hegyi competition index was significantly higher for HO with respect to pines, whereas no significant differences were found between NDP, DFP and DP (Curiel Yuste et al. 2012).

The root-excision method (Subke et al. 2006) was used for studying total, autotrophic and heterotrophic soil respiration, using the protocol proposed by Heinemeyer et al. (2007). Three different polyvinylchloride (PVC) collars (treatment collars) of 63 cm in diameter were installed within 3 m of each tree (Fig. 1). The first type of collar (A) was 5 cm in height and was inserted only 2 cm into the ground and fixed with three metal sticks. Thus, these A-type collars did not interfere with fine roots, mycorrhizal or soil microbial dynamics and growth. The second and the third types of collar (B and C, respectively) were 50 cm in height and were inserted to a depth of 45 cm into the soil. Collar B had four rectangular windows (17 × 5 cm) at 10 cm from the top, covering 33 % of the total collar perimeter. The windows were covered with nylon fabric of 41-μm mesh, allowing ingrowth of fungal hyphae but not of roots (Ek 1997). The deeper B-type collars prevented the ingrowth of fine roots (which are concentrated mainly in the upper centimetres of the soil (Jackson et al. 1997). C-type collars were the same size and were installed at the same depth as B-type collars, but they did not have windows, so prevented the ingrowth of both fine roots and mycorrhizal hyphae. Hence, we assumed that in C-type collars, only the non-rhizospheric microbial community remained active.

Due to the great stoniness of the soil, two modifications were made to the Heinemeyer et al. (2007) experimental design. First, treatment collars were bigger (20 cm in diameter in the original protocol), and second, we dug a hole in the soil prior to the installation of the deeper collars. After placing the collar inside the hole, we filled the space inside the collar with the previously removed soil material, preserving the original soil-horizon order. Two smaller PVC collars (sampling collars; 10 cm diameter and 4 cm height)
were installed as replicate collars within each treatment collar. Sampling collars were inserted 1 cm into the ground and fixed with polyurethane foam. These collars delimited the reference surface of our soil respiration measurements. Collar installation was done 14 months before the start of measurements in order to minimize the effects of soil disturbance on soil respiration measures.

**Measurements**

Soil respiration rates were measured with a close-path infra-red gas analyser coupled to a closed dynamic chamber (EGM-4 and SRC-1; PP-Systems, Hitching, UK) in the sampling collars (the soil chamber fitted well with the small collars because it had the same diameter). Soil respiration was measured every 2 weeks during 1 year, from June 2012 to June 2013 (25 campaigns). For each campaign, five rounds of measurements were made for all 72 small collars during 24 h, in order to capture the soil respiration variability associated with daily cycles. One round was started 2 h before sunrise, another was performed after sunset and the others were equally distributed during the daytime. Since soil respiration was manually measured, the effort to integrate the spatial variability of soil respiration in this extremely rocky location and also the daily soil respiration course did not allow us to increase the number of measured trees.

Soil temperature at 10 cm was measured once per big collar and per round of measurements using a thermometer (HH806AU; OMEGA, Stamford). SWC in the top 15 cm was measured in each campaign at each tree by time domain reflectometry (TDR) (Tektronix 1502C; Beaverton, Oregon). One 15-cm-long TDR probe was permanently installed vertically in the upper soil close to each tree throughout the experiment. In order to correct the SWC measurements for stoniness, gravimetrical SWC measured in soil samples close to the TDR probes were regressed against TDR measurements [for more information, see Poyatos et al. (2013)].

One litterfall trap (555 \( \times \) 355 mm) was installed within 2 m of each tree and litterfall was collected during every campaign, dried for 24 h at 70 °C and weighed.

Air temperature and relative humidity were continuously measured in a meteorological tower installed less than 100 m from the farthest tree. Continuous SWC was also recorded in the upper 30 cm of soil using four frequency domain reflectometers (CS616; Campbell Scientific, Logan, UT) randomly distributed among the trees. A data-acquisition system (CR1000 datalogger and AM16/32 multiplexers; Campbell Scientific) was used to store 15-min means of soil moisture and meteorological variables sampled every 30 s.

**Data analysis**

**Soil respiration calculation**

The five soil respiration measurements recorded for each small collar were time-averaged in order to obtain mean daily soil respiration. Then, both replicates were averaged at the big collar level (A, B and C; Fig. 1).

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R_S; R_H; R_A; R_R; R_M.
\]

\( R_S \) and \( R_H \) were estimated directly as the soil respiration rates measured in collars A and C, respectively. \( R_A \) was calculated by subtracting C from A; \( R_R \) by subtracting B from A; and \( R_M \) by subtracting C from B.

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**Fig. 1** Root-exclusion experimental design. Large collars depict the different exclusion treatments for soil CO\(_2\) efflux measurements. Small collars are pseudoreplicates within treatments and small rectangles in b represent the mesh allowing mycorrhizae ingrowth. a Roots and mycorrhizae included, b roots excluded and mycorrhizae included, c roots and mycorrhizae excluded
Soil respiration drivers

Mixed-effects models were used to analyse the relationships between soil respiration and type of tree, soil temperature, SWC, litterfall and season with campaign data. The limits of seasons were adjusted from environmental variables (i.e. summer ended with the first rainfall events in fall, which changed drastically SWC and temperature). Linear and exponential relationships between soil respiration and temperature were tested in the models, as well as linear and quadratic relationships between soil respiration and SWC. In all cases, the linear relationships performed better than the nonlinear transformations according to the corrected Akaike information criterion statistic (data not shown).

Different models were fitted for each soil respiration component (\(R_s\), \(R_h\), \(R_a\), \(R_m\) and \(R_r\)). As all variables were measured near the same trees throughout the campaigns, tree identity was included as a random factor in all models. Models with all combinations of predictor variables and their second-order interactions were performed, and the best model in terms of corrected Akaike information criterion was selected. To determine the variability explained by each mixed model, we calculated the coefficient of determination using the log likelihood of both the studied model and the null model (which did not include any predictor variables). In the root-exclusion method, the PVC collars could interfere with soil temperature and moisture (Kuzyakov 2006). Unfortunately, due to instrumental limitations, SWC was only measured at tree level (and not at collar level) in each campaign. SWC was gravimetrically measured in samples inside the 72 small collars at the end of the experiment (July 2013) and one-way ANOVA was performed to test for differences in SWC between the different treatment collars.

Annual SR

We used the models fitted in 2.3.2 to estimate daily values of \(R_s\), \(R_h\), \(R_a\), \(R_m\) and \(R_r\) for a whole year (from mid-June 2012 to mid-June 2013). Apart from fixed predictors (season, type of tree), daily aggregated values of soil temperature, SWC and litterfall were needed as inputs for the model. For each tree and collar type, linear regressions were fitted between daily averaged soil temperature measured during the campaigns and simultaneous air temperature measured at the meteorological tower (\(R^2 = 0.93 \pm 0.02\), across-trees mean \(\pm\) SD). Likewise, daily SWC for each tree was estimated from linear regressions against mean SWC measured with the four frequency domain reflectometers near the meteorological tower (\(R^2 = 0.66 \pm 0.27\), across-trees mean \(\pm\) SD). Daily litterfall across trees was linearly interpolated from litterfall measured biweekly. Modelled values of daily \(R_s\), \(R_h\), \(R_a\), \(R_m\) and \(R_r\) were then aggregated to obtain annual values.

Mixed-effects models, including tree identity as a random factor, were then used to analyse the differences in annual soil respiration and its components between types of tree. Given the high spatial variability of soil respiration, especially in this ecologically complex site (Barba et al. 2013), and the limited number of replicates (three trees per type), we considered marginally significant differences among means when \(0.05 < p < 0.1\). Additionally, a Friedman test and its post hoc analysis were applied to the daily averaged data from the 25 campaigns, to test for possible differences in soil respiration and its components between types of tree. The Friedman test is a non-parametric repeated-measure ANOVA. Its procedure involves ranking soil respiration from the different tree types and then considering the values of ranks by campaigns.

To test whether the relative contribution of \(R_h\)–\(R_m\) increases along the die-off process, mixed-effects models with tree type (for testing annual differences) or with the interaction between tree type and season (for testing differences over seasons) were used, including tree identity as a random factor. Heterotrophic relative contribution data were log transformed to achieve normality.

All the analyses were carried out using R 3.0.3. (R Foundation for Statistical Computing, Vienna). The mixed-effects models were performed using the R package nlme (Pinheiro et al. 2009) and the step-wise model selection was performed with the MuMIn package (Bartón 2014).

Results

Seasonal course of environmental variables and soil respiration components

Over the study period, climate was typical of a low-elevation Mediterranean mountain, with mean air temperature of 11.2 °C, annual precipitation of 703 mm and a relatively dry summer (93 mm from June to September and mean SWC below 15 % from mid-July to the end of September) (Fig. 2b, c). The seasonal pattern of litterfall was not as clear as those of temperature and SWC, but it seemed to peak at the end of fall (Fig. 2d).

No significant differences were found for soil temperature, SWC and litterfall among types of trees (Table 1). While type of collar did not influence soil temperature during the experiment (\(p = 0.87\), repeated-measures ANOVA), SWC measured gravimetrically at the end of experiment (July 2013) was higher for deeper collars (B and C) than for surface ones (A) (\(p = 0.03\), one-way ANOVA), 3.4 % on average.
$R_S$ flux peaked during late spring and early summer (up to 6 µmol m$^{-2}$ s$^{-1}$; Fig. 3a) and then decreased over the course of the summer to 33% of peak values. During fall and winter, $R_S$ was quite low (between 0 and 2 µmol C m$^{-2}$ s$^{-1}$). $R_H$ showed a similar annual pattern to $R_S$ with values ranging between 1 and 4 µmol C m$^{-2}$ s$^{-1}$ (Fig. 3b). No seasonal pattern was observed either for $R_A$, or for its components ($R_M$ and $R_R$) (Fig. 3c, d). Soil CO$_2$ efflux measured in HO was the lowest in 88% of the campaigns for $R_S$, 76% for $R_H$, 68% for $R_A$, 56% for $R_R$, but only in 24% of the campaigns for $R_M$ (Fig. 3). Indeed, the non-parametric Friedman test applied to the campaign data indicated that respiration rates under HO were lower than under the three types of pines for $R_S$, $R_H$, $R_A$, and $R_R$ ($p < 0.001$ for $R_S$ and $R_H$, $p = 0.001$ for $R_A$, $p = 0.002$ for $R_R$), but not for $R_M$.

The relative contribution of $R_H$ to $R_S$ did not show differences among tree types, either at annual ($p = 0.968$) or at
Table 1 Environmental variables during the study period summarized by type of tree (mean and SD)

|                      | NDP | SD  | DFP | SD  | DP  | SD  | HO  | SD  |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|
| Temperature (°C)     | 11.68| 0.29 | 11.70| 0.68 | 12.00| 0.40 | 11.21| 0.14 |
| SWC (cm³ cm⁻³)       | 20.20| 0.04 | 20.21| 0.06 | 20.21| 0.02 | 20.20| 0.05 |
| Litterfall (g m⁻² day⁻¹) | 1.84| 0.67 | 1.19 | 0.11 | 1.92 | 0.89 | 1.96 | 0.19 |

No differences were found between type of tree (p < 0.05, mixed-effects model with tree as a random factor)

NDP Non-defoliated pines, DFP defoliated pines, DP dead pines, HO holm oaks, SWC soil water content

Fig. 3 Annual soil respiration evolution and its components. a Total soil respiration (Rₛ), b heterotrophic respiration (R₉), c root respiration (Rᵣ), d mycorrhizal respiration (Rₘ). Each symbol represents the average of five measurements within a 24-h cycle and the three trees of each type. Campaign-specific error bars were not drawn for better clarity. NDP Non-defoliated pines (blue inverted triangle), DFP defoliated pines (black square), DP dead pines (red circle), HO holm oaks (green triangle) (color figure online)
seasonal scales ($p = 0.325$) (generalised linear models with tree identity as a random factor). Nonetheless, the relative contribution of the different soil respiration components considering all tree types together varied during the year. The contribution of $R_H$ to $R_S$ was highest during late winter, spring and summer, and decreased during fall and early winter. In contrast, the contribution of $R_R$ to $R_S$ increased during fall and early winter. The contribution of $R_M$ to $R_S$ did not show any seasonal pattern, remaining low throughout the year (Fig. 4).

**Soil respiration drivers**

A mixed-effects model including the interactions between season-SWC-temperature and temperature-type of tree as predictor variables (Table 2, $R_S$) explained 51 % of the seasonal variability in $R_S$. The higher the SWC, the larger the positive effect of temperature on $R_S$, especially during spring and summer. However, at SWC values below 10 %, the temperature effect on $R_S$ was negligible in summer (Fig. 5i–l). Additionally, SWC had a higher effect on $R_S$ under HO than under pines. Similarly, tree type interacted with SWC to determine $R_H$, while the rest of the $R_H$ predictors were almost the same as those in the $R_S$ model (Table 2, $R_H$ and Fig. 6). The $R_H$ model explained 56 % of the total variability in $R_H$. The interaction between SWC and temperature had the same positive effect as in the $R_S$ model (higher effect of temperature at high SWC values). Temperature had the lowest effect on $R_H$ during fall and winter, a higher effect during summer and the highest effect during spring (Table 2).

Models of the autotrophic components of $R_S$ explained much less variability than the ones fitted for $R_S$ and $R_H$. The selected $R_A$ model was able to explain only 15 % of the autotrophic respiration variability, and included the positive effect of litterfall and the positive interaction between SWC and temperature (Table 2). Likewise, the selected $R_R$ model was able to explain only 13 % of the variability in $R_R$ and contained the interactions season-SWC and season-temperature (Table 2). Finally, the selected $R_M$ model was able to explain 24 % of the variability in mycorrhizal respiration and contained only the interaction between SWC-temperature (Table 2). Type of tree had no effect on $R_A$, nor on its fractions ($R_R$ and $R_M$).

**Annual $R_S$ and its components**

For the overall set of sampled trees, modelled annual $R_S$ (mean ± SD) from July 2012 to July 2013 was $2.6 \pm 0.6$ µmol m$^{-2}$ s$^{-1}$, $R_H$ was $1.7 \pm 0.3$ µmol m$^{-2}$ s$^{-1}$, representing 65 % of $R_S$, while $R_A$ was $1.0 \pm 0.5$ µmol m$^{-2}$ s$^{-1}$ (36 % of $R_S$). $R_R$ and $R_M$, as components of $R_A$, were $0.6 \pm 0.6$ µmol m$^{-2}$ s$^{-1}$ (23 % of $R_S$) and $0.3 \pm 0.7$ µmol m$^{-2}$ s$^{-1}$ (13 % of $R_S$), respectively.

The mixed-effects models showed that annual $R_S$ under HO was marginally lower than under NDP ($p$-value 0.074) (64 % on average), whereas DFP and DP did not show differences with NDP or HO. Likewise, annual $R_H$ under HO was significantly lower than under NDP ($p$-value 0.030; 36 % lower), and marginally significantly lower than under DFP ($p$-value 0.089; 23 % lower) and DP ($p$-value: 0.054;
Table 2 Summary of the selected model of total soil respiration ($R_t$), heterotrophic respiration ($R_h$), autotrophic soil respiration ($R_a$), fine-root respiration ($R_r$) and mycorrhizal respiration ($R_m$)

| Variables                  | Estimate | SE   | t-value | p-value |
|----------------------------|----------|------|---------|---------|
| $R_t$                      |          |      |         |         |
| Intercept                  | 6.971    | 2.016| 3.458   | 0.001   |
| SWC                        | −0.563   | 0.145| −3.888  | <0.001  |
| Temperature                | −0.412   | 0.109| −3.798  | <0.001  |
| Summer                     |          |      |         |         |
| Fall                       | −8.275   | 3.410| −2.427  | 0.016   |
| Winter                     | −5.869   | 2.640| −2.223  | 0.027   |
| Spring                     | −4.132   | 3.392| −1.218  | 0.224   |
| HO                         |          |      |         |         |
| NDP                        | 1.102    | 0.669| 1.647   | 0.138   |
| DFP                        | 0.426    | 0.673| 0.633   | 0.545   |
| DP                         | 0.287    | 0.664| 0.433   | 0.677   |
| SWC × temperature          | 0.044    | 0.008| 5.356   | <0.001  |
| Season                     |          |      |         |         |
| Summer                     |          |      |         |         |
| Fall                       | 0.093    | 0.028| 3.331   | 0.001   |
| Winter                     | 0.081    | 0.032| 2.577   | 0.011   |
| Spring                     | 0.007    | 0.002| 3.850   | <0.001  |
| Temperature × type         |          |      |         |         |
| Temperature × HO           | −0.024   | 0.027| −0.881  | 0.379a  |
| Temperature × NDP          | 0.016    | 0.027| 0.608   | 0.544ab |
| Temperature × DFP          | 0.051    | 0.026| 1.963   | 0.051b  |
| Season × SWC               |          |      |         |         |
| Sum × SWC × temperature    |          |      |         |         |
| Fall × SWC × temperature   | −0.050   | 0.015| −3.453  | 0.001b  |
| Win × SWC × temperature    | −0.043   | 0.015| −2.875  | 0.004b  |
| Spr × SWC × temperature    | −0.029   | 0.015| −1.949  | 0.052ab |
| $R_h$                      |          |      |         |         |
| Intercept                  | −0.734   | 0.578| −1.270  | 0.205   |
| SWC                        | −0.032   | 0.029| −1.088  | 0.278   |
| Temperature                | 0.027    | 0.033| 0.826   | 0.410   |
| SWC × temperature          | 0.009    | 0.002| 1.146   | 0.000   |
| Season                     |          |      |         |         |
| Summer                     |          |      |         |         |
| Fall                       | 1.344    | 0.617| 2.179   | 0.030   |
| Winter                     | 1.455    | 0.574| 2.536   | 0.012   |
| Spring                     | −0.079   | 0.586| −0.133  | 0.894   |
| $R_a$                      |          |      |         |         |
| Intercept                  | 1.286    | 0.544| 2.366   | 0.019   |
| SWC                        | −0.081   | 0.032| −2.511  | 0.013   |
| Temperature                | 0.005    | 0.002| 3.076   | 0.002   |

HO and Summer are used as the reference categories and are included in the intercept. Different lowercase letters indicate significant differences between levels of predictor variables. For other abbreviations, see Table 1.
affect the relative contribution of heterotrophic respiration did not support what we had hypothesized (hypothesis 1). Therefore, also associated with major changes in soil respiration (both heterotrophic and autotrophic activity; see Fig. 7), contrary to what we had hypothesized (hypothesis 1). Therefore, also the relative contribution of heterotrophic respiration did not increase from NDP to DFP and DP. Defoliation did not affect $R_S$ or its components with respect to NDP. Moreover, 3–11 years after tree death, we observed that $R_S$ (and all its components) associated with DP had either completely recovered or remained unchanged (Fig. 7). Even the autotrophic components ($R_R$ and $R_M$) of $R_S$, directly dependent on the substrate inputs from plant photosynthetic activity (e.g. Högb erg et al. 2001), were not affected along this die-off gradient. These effects are surprising, given that soil autotrophic respiration had been reported to be extremely sensitive to decreases in photosynthetic activity associated with defoliation and die-off (Levy-Varon et al. 2012, 2014; Moore et al. 2013; Borkhuu et al. 2015). Indeed, decreases in plant productivity have been associated with lower fine root biomass and hence lower root metabolic activity, lower belowground substrate allocation and lower root exudation, all contributing to lower $R_A$ and its fractions (Högb erg and Read 2006).

We did not find higher $R_H$ under DP than under NDP, which is consistent with the fact that tree mortality did not apparently result in higher soil moisture, soil temperature or litterfall under dead pines, factors which are known to stimulate $R_H$. Although the relative contribution of $R_H$ to $R_S$ (and thus, also $R_A$) showed a clear seasonal pattern, this pattern was preserved across the entire pine die-off gradient (NDP, DFP and DP).

The stability in $R_S$ and in its fractions along the pine die-off gradient denotes a high degree of resilience of soil processes with respect to aboveground perturbations. Some studies have also shown that $R_S$ remained stable after a perturbation (Binkley et al. 2006; Levy-Varon et al. 2014), suggesting that this $R_S$ resilience could be produced by mobilization of reserve carbohydrates (Levy-Varon et al. 2012), by a higher growth rate of non-disturbed trees (Levy-Varon et al. 2014), suggesting that an increment of $R_H$ due to an increment in organic matter availability could be compensating for a decrease in $R_A$ (Borkhuu et al. 2015). While this has been partially shown in some studies (Levy-Varon et al. 2012, 2014; Moore et al. 2013; Borkhuu et al. 2015), here we present, to the best of our knowledge, the very first evidence that all the components of $R_S$ remain apparently unaffected after 10 years of drought-related mortality processes.

Our results might be partially explained by the disturbance recovery findings in Nave et al. (2011), which suggest that a short perturbation of forest C cycling due to partial canopy disturbance could be rapidly recovered (within a few years), thereby stabilizing the C cycle. Nave et al. (2011) hypothesize that shortly after the perturbation, the expected decrease in ecosystem production and soil respiration (due to decrease fine root biomass and non-structural carbohydrate concentrations in roots) could be compensated for by higher growth rates of the remaining healthy trees due to reduced competition for limiting resources. At the study site, after drought-induced pine mortality in the 1990s, higher growth rates of the remaining healthy trees were observed (Martínez-Vilalta and Píñol 2002), consistent with this hypothesis.

The mechanism underlying the observed resilience of $R_S$ following Scots pine die-off is likely more related to belowground colonization by HO than to the remaining,

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**Discussion**

**Annual soil respiration and its fractions**

Mean annual $R_S$ at the study site was 2.6 µmol m$^{-2}$ s$^{-1}$, similar to values reported for a parallel valley in the same nature reserve [2.3 µmol m$^{-2}$ s$^{-1}$ (Asensio et al. 2007)]. $R_H$ was the most important fraction of $R_S$, representing about 65%. This relative importance agrees well with estimates obtained in other forest ecosystems (Rey et al. 2002; Tedeschi et al. 2006; Heinemeyer et al. 2007; Subke et al. 2011), confirming the important role of microbial soil respiration in $R_S$. The $R_R$ and $R_M$ contributions to $R_S$ (23 and 13%, respectively) were also similar to values reported in other partitioning studies (Malhi et al. 1999; Rey et al. 2002; Subke et al. 2006; Heinemeyer et al. 2007; Ruehr and Buchmann 2010).

**Soil respiration and its components following Scots pine die-off**

Scots pine die-off, from NDP to DFP and DP, was not associated with major changes in soil respiration (both heterotrophic and autotrophic activity; see Fig. 7), contrary to what we had hypothesized (hypothesis 1). Therefore, also the relative contribution of heterotrophic respiration did not increase from NDP to DFP and DP. Defoliation did not affect $R_S$ or its components with respect to NDP. Moreover, 3–11 years after tree death, we observed that $R_S$ (and all its components) associated with DP had either completely recovered or remained unchanged (Fig. 7). Even the autotrophic components ($R_R$ and $R_M$) of $R_S$, directly dependent on the substrate inputs from plant photosynthetic activity (e.g. Högb erg et al. 2001), were not affected along this die-off gradient. These effects are surprising, given that soil autotrophic respiration had been reported to be extremely sensitive to decreases in photosynthetic activity associated with defoliation and die-off (Levy-Varon et al. 2012, 2014; Moore et al. 2013; Borkhuu et al. 2015). Indeed, decreases in plant productivity have been associated with lower fine root biomass and hence lower root metabolic activity, lower belowground substrate allocation and lower root exudation, all contributing to lower $R_A$ and its fractions (Högb erg and Read 2006).

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The stability in $R_S$ and in its fractions along the pine die-off gradient denotes a high degree of resilience of soil processes with respect to aboveground perturbations. Some studies have also shown that $R_S$ remained stable after a perturbation (Binkley et al. 2006; Levy-Varon et al. 2014), suggesting that this $R_S$ resilience could be produced by mobilization of reserve carbohydrates (Levy-Varon et al. 2012), by a higher growth rate of non-disturbed trees (Levy-Varon et al. 2014), suggesting that an increment of $R_H$ due to an increment in organic matter availability could be compensating for a decrease in $R_A$ (Borkhuu et al. 2015). While this has been partially shown in some studies (Levy-Varon et al. 2012, 2014; Moore et al. 2013; Borkhuu et al. 2015), here we present, to the best of our knowledge, the very first evidence that all the components of $R_S$ remain apparently unaffected after 10 years of drought-related mortality processes.

Our results might be partially explained by the disturbance recovery findings in Nave et al. (2011), which suggest that a short perturbation of forest C cycling due to partial canopy disturbance could be rapidly recovered (within a few years), thereby stabilizing the C cycle. Nave et al. (2011) hypothesize that shortly after the perturbation, the expected decrease in ecosystem production and soil respiration (due to decrease fine root biomass and non-structural carbohydrate concentrations in roots) could be compensated for by higher growth rates of the remaining healthy trees due to reduced competition for limiting resources. At the study site, after drought-induced pine mortality in the 1990s, higher growth rates of the remaining healthy trees were observed (Martínez-Vilalta and Píñol 2002), consistent with this hypothesis.

The mechanism underlying the observed resilience of $R_S$ following Scots pine die-off is likely more related to belowground colonization by HO than to the remaining,
Drought-induced substitution of Scots pine by holm oak causes a decrease in soil respiration

Changes in vegetation could produce changes in the whole plant-to-soil system, such as root biomass and distribution, nutrients and water balance, net primary production, carbohydrate allocation patterns, litter quantity and quality, decomposer community or microbial diversity (Jackson et al. 1997; Binkley and Giardina 1998; Palacio et al. 2007; Strickland et al. 2009; Curiel Yuste et al. 2012), which in turn could modify $R_S$ and its heterotrophic and autotrophic fractions (Uren 2000; Janssens et al. 2001; Kuzyakov 2006; Cornwell et al. 2008; Vivanco and Austin 2008). Despite the strong resilience of $R_S$ and its components along the Scots pine die-off (NDP, DFP and DP) (see “Soil respiration and its components following Scots pine die-off”), changes in $R_S$ associated with the succession from Scots pine to holm oak were observed. Annual $R_S$ was 36 % lower in HO compared to NDP, contrary to our hypothesis 2. Although the analysis of annual values did not show differences in $R_A$, $R_R$ or $R_M$ between NDP and HO (Fig. 7), seasonal data analysed with the non-parametric Friedman test suggested lower values for $R_A$ and $R_R$ under HO. However, the magnitude of these differences was small (Fig. 3) and the differences in $R_S$ between HO and NDP

unaffected, pines. Results obtained from previous studies in the same site support this idea. Firstly, spatial variability of $R_S$ close to dead pines has been mainly associated with the spatial distribution of HO basal area (Barba et al. 2013) suggesting a functional colonization by the HO rhizosphere. Moreover, it has been observed that rates of $R_R$ measured in living roots under DP were similar to those measured for HO (Pereira-Blanco 2014), which suggests that fine root colonization of the disturbed gap is taking place by HO. Finally, Curiel Yuste et al. 2012 found that there was a similarity in the most abundant bacterial taxa (i.e. Actinomycetales, Rhizobiales, Xanthomonadales) between rhizosphere from DP and HO, indicating that HO colonization is also occurring at the microbial level.
were apparently more related to differences in $R_H$ (36% lower in HO than in NDP). But the vegetation effect on $R_S$ was not indirect via modifications in the environmental conditions (as we expected in hypothesis 3b), since no differences were found in SWC or soil temperature along the die-off stages or between species. These differences in $R_S$ were apparently more related to differences in $R_H$ (36% lower in HO than in NDP). But the vegetation effect on $R_S$ was not indirect via modifications in the environmental conditions (as we expected in hypothesis 3b), since no differences were found in SWC or soil temperature along the die-off stages or between species. These differences in $R_S$...
were probably driven by changes in microbial community composition and functional diversity. This conclusion is supported by (1) the observed species-specific microbial community under each type of tree at the study site and the lack of differences in soil environmental conditions and in soil C pools (both quality and quantity) (Curiel Yuste et al. 2012), and (2) by the different functional diversity of the decomposer community between types of tree as observed in a litter decomposition experiment in the same study site (Barba et al. 2015).

This shift towards lower $R_s$ under holm oak following Scots pine drought-induced mortality could have crucial implications for the C balance of this particular ecosystem and, by extension, for the C cycling in Mediterranean drought-exposed Scots pine forests where a gradual replacement by Quercus species is increasingly being reported (Martínez-Vilalta et al. 2012; Galán et al. 2013; Vilà-Cabrera et al. 2013; Carnicer et al. 2014). However, we are aware that this study has been performed with a limited number of replicates, and studies addressing this question at the ecosystem level are required in order to make more reliable projections. Additionally, selecting individual trees as the experimental unit allows the comparison of soil respiration and its components between different types of trees, but hinders the extrapolation of the results to the forest level.

**Environmental controls of autotrophic and heterotrophic soil respiration along a die-off gradient and species succession**

The interactions between season-SWC-temperature and temperature-type of tree were able to explain 51% of the $R_s$ variability. The positive interaction between SWC and temperature indicated that the higher the SWC, the higher the temperature effect, and had similar effects on $R_H$, $R_R$ and $R_M$ fluxes. However, only during part of the springtime were there simultaneous high SWC and temperature values (see Fig. 2). We did not find support for our hypothesized higher sensitivity of $R_s$ and $R_A$ to SWC under Scots pine (hypothesis 2). On the contrary, we observed a higher sensitivity of $R_H$ to SWC under HO (Table 2; Fig. 6), which could be due to a better adaptation to the strong seasonal changes in water availability of the microbial community associated with this typical Mediterranean species (Curiel Yuste et al. 2014) or to higher microbial biomass under HO resulting in a higher response to changes in SWC.

While environmental variables have been described as major drivers of $R_A$ at the global scale (Piao et al. 2010), vegetation activity has been usually described as the most determinant factor for $R_s$ at the ecosystem scale (Janssens et al. 2001; Tang et al. 2005; Högborg et al. 2009). Therefore, the limited explanatory power of environmental variables on autotrophic component models obtained in this study (and expected in hypothesis 3a) could be explained by the lack of variables reflecting properly the photosynthetic activity of trees. Indeed a parallel study in the same area has shown that variations in $R_R$ at the tree level were positively correlated with the sap flow of the same trees (Pereira-Blanco 2014). This highlights the need for further studies on the dependency of $R_s$ and its components on aboveground plant productivity (and not only on environmental variables), both measured at stand level, to understand the ecosystem mechanisms used to cope with climate-driven disturbances.

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**Author contribution statement** J. B., J. C. Y. and F. L. L. conceived and designed the experiment; J. B., J. C. Y. and R. P. performed the experiment; J. B., J. C. Y., I. J. and R. P. analysed the data; J. B. wrote the paper and all authors edited the manuscript.

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