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An overview of the forests' health status in the Port-Cros National Park (Provence, France)

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Abstract. Mediterranean forests are currently undergoing a process of decline as evidenced by decreasing tree growth rates, increasing leaf deficit and tree mortality rates. This is mainly attributed to increasing drought stress induced by climate change, and may have significant impacts on the services they provide to human society. In this context, we evaluated the health of the forests in the Port-Cros National Park in 2023 based on 36 plots, and the biotic and abiotic factors associated with forest decline.

This assessment revealed significant tree leaf deficit and mortality rates, indicating widespread decline. Notably, 68% of *Quercus ilex* and 64% of *Quercus suber* trees were classified as declining as they showed a leaf deficit above 50%, surpassing regional averages. In contrast, only 14% of *Pinus halepensis* trees were declining, with a mean leaf deficit of 36%. Tree mortality rates were notably high, with 12% of basal area and 18% of stems affected, far exceeding France's national average of 5%, and were higher for understorey shrubs (*Arbutus unedo* and *Erica arborea*) compared to overstorey species.

Drought was identified as a key driver causing forest decline, exacerbated by rising temperatures since the 1980s. Indeed, stands growing on soils with high water content showed higher mean leaf deficit. Dense stands with high basal area experienced higher mortality, and smaller trees or shade-intolerant shrubs showed the greatest vulnerability. Beyond climate, stand densification and self-thinning processes have thus contributed to forest decline. Given the low variability of the observed decline rates between plots and the limited sampled environmental gradient, it seems necessary to conduct more in-depth studies at larger scales to better discern the influence of each biotic and abiotic factor.

Keywords: forest decline, Mediterranean, tree mortality, drought.

***Résumé*. Un aperçu de l'état de santé des forêts dans le parc national de Port-Cros (Provence, France).** Les forêts méditerranéennes subissent actuellement un processus de déclin, comme en témoignent la diminution des taux de croissance des arbres, l'augmentation des taux de déficit foliaire et des taux de mortalité des arbres. Ce phénomène est principalement attribué à l'augmentation du stress lié à la sécheresse induit par le changement climatique, et peut avoir des impacts significatifs sur les services fournis par les forêts à la société humaine. Dans ce contexte, nous avons évalué la santé de 36 parcelles forestières du parc national de Port-Cros en 2023, ainsi que les facteurs biotiques et abiotiques associés au déclin des forêts.

Cette évaluation a révélé des taux importants de déficit foliaire et de mortalité des arbres, indiquant un déclin généralisé. En particulier, 68 % des chênes verts (*Quercus ilex*) et 64 % des chênes liège (*Quercus suber*) ont été classés comme étant en déclin car ils présentaient un déficit foliaire supérieur à 50 %, ce qui dépasse les moyennes régionales. En revanche, seuls 14 % des pins d'Alep (*Pinus halepensis*) étaient en déclin, avec un déficit foliaire moyen de 36 %. Les taux de mortalité des arbres étaient particulièrement élevés, avec 12 % de la surface terrière et 18 % des tiges touchées, ce qui dépasse de loin la moyenne nationale française de 5 %, et étaient plus élevés pour les arbustes du sous-étage (*Arbutus unedo* et *Erica arborea*) que pour les espèces de l'étage supérieur.

La sécheresse a été identifiée comme l'une des principales causes du déclin des forêts, exacerbée par l'augmentation des températures depuis les années 1980. En effet, les peuplements poussant sur des sols à forte teneur en eau présentaient un déficit foliaire moyen plus élevé. Les peuplements denses avec une surface de base élevée ont connu une mortalité plus élevée, et les arbres plus petits ou les arbustes intolérants à l'ombre ont montré la plus grande vulnérabilité. Au-delà du climat, la densification des peuplements et les processus d'auto-éclaircissement ont donc contribué au déclin des forêts. Étant donné la faible variabilité des taux de dépérissement observés entre les placettes et le gradient environnemental échantillonné limité, il semble nécessaire de mener des études plus approfondies à des échelles plus larges pour mieux discerner l'impact de chaque facteur biotique et abiotique.

Mots-clés : dépérissement forestier, Méditerranée, mortalité des arbres, sécheresse.

Introduction

Forests contribute to human well-being in several ways, for instance by sequestering carbon, producing wood, or regulating the water cycle. In protected areas partially opened to tourism, they are also important as a source of recreation, inspiration, and a reservoir of plant and animal biodiversity. These services are tightly associated with forest functioning, e.g., with the capacity of individual trees to absorb carbon through photosynthesis, and with forest demography including tree regeneration, growth and mortality rates. However, these processes are currently strongly impacted by climate change: the negative effects of increasing drought frequency and intensity on vegetation are large and not compensated by the positive effects of CO_2 fertilization and increasing length of the growing season (e.g., Song *et al.,* 2024; Walker *et al.,* 2021).

The impacts of climate change on forest functions is especially perceptible in the Mediterranean area, which is subjected to a rise in temperatures faster than the global average (Guiot and Cramer, 2016), and consequently an increase in drought stress. Several studies report a decrease in tree growth rates, for instance in Spain (Galvan *et al.,* 2014) and in other Mediterranean countries (e.g., Sarris *et al.,* 2007). Trees also tend to produce a lower number of leaves and smaller leaves to reduce the water demand and use, which explain the gradual increase in leaf deficit since the 1990s (Carnicer *et al.,* 2011). This decline in tree vitality can lead to tree death if the drought stress is too long and/or intense, and can be exacerbated by pests and pathogens outbreak and infestations. Indeed, several hot-spots of drought-induced mortality have been observed in the Mediterranean regions over the last decades (Allen *et al.,* 2015; Neumann *et al.,* 2017).

Even though the South of France is not the French region the most affected by the decline in tree vitality (e.g., spruce mortality due to bark-beetles in North-East; decline of oaks and ink disease on chestnut in central France; DSF, 2023), the situation is not rosy. According to the French Forest Health Department (DSF), 21% of the trees had a leaf deficit over 50% in 2023 (DSF, 2024), a threshold above which specialists usually consider that a tree is declining (Lemaire *et al.,* 2022). Some species are particularly concerned such as *Pinus sylvestris* Linnaeus in the Pre-Alps, where 31% of the trees were classified as declining in 2017 (Lemaire *et al.,* 2022), and an excess mortality has been observed (Taccoen *et al.,* 2022). Even the species that are more drought tolerant are impacted. For instance, 51% of the *Quercus suber* Linnaeus trees were declining in 2023, a proportion that increased regularly from 20% to 50% in 10 years, with peaks in 2015, 2020 and 2023 (DSF, 2024). For *Quercus ilex* L., 41% of the trees were declining in 2019, while it was only 5% in 2000 (Bec *et al.,* 2020); a comparable temporal trend being observed in *Pinus halepensis* Miller (GREC-SUD, 2024).

Given the speed of the observed decline in tree vitality in the South of France and its potentially strong impact on forests, it is fundamental to (i) evaluate the current health state of the forest and (ii) identify the abiotic and biotic factors associated with tree decline. This is especially important as Mediterranean forests provide diversified contributions to society (Gauquelin *et al.,* 2018). They contain a large fraction of the forest plant richness of Metropolitan France, with almost twice as many species in Mediterranean forests than in European temperate forests (247 compared with 135; Quézel and Médail, 2003). This diversity is particularly high in regional or national parks, such as the Port-Cros National Park, because of the protection measures that have been implemented, which makes these areas essential. Based on dendrometric surveys and visual observations of (co-)dominant trees, we evaluated the rates of branch and tree mortality in 36 plots in the Port-Cros National Park and estimated the leaf deficit of its main tree species: *Pinus halepensis*, *Quercus ilex* and *Quercus suber*. Then, we assessed the impact of multiple environmental factors (soil, topography, stand characteristics) on these forest health indicators using mixed-effects models. By combining this monitoring of forest health with a statistical modelling approach, we aimed at improving our understanding of the dieback process affecting Mediterranean forest tree species and our ability to predict the areas at risk.

Materials and Methods

Study area and plots

We selected 36 plots located within the boundaries of the Port-Cros National Park (PCNP) that cover a broad environmental spectrum in terms of topography, soil, and stand characteristics (excluding the Port-Cros Island; Fig. 1). 27 plots were selected from the 150+ plots established in 1996 on the Porquerolles Island by the PCNP to monitor the forest habitats (following the protocol of dendrometric monitoring of the forest reserves; PSDRF), while 9 were installed on the continental part of the PCNP to include stands dominated by *Q. suber* (see Figs. 1 and S2). We specifically focused on forested areas dominated by *P. halepensis*, *Q. ilex* and/or *Q.suber*, excluding stands dominated by shrubs such as *Arbutus unedo* Linnaeus and *Erica arborea* Linnaeus. All plots were precisely georeferenced to enable future monitoring, and to get accurate Geographic Information System (GIS) data (see below).

Mean annual rainfall in the study area is 621 mm while mean annual temperature is 12.7°C (1950-2023 period; data for the Porquerolles Island; see Fig. S1). The bioclimate is typically Mediterranean with a summer drought from June to August, with most of the precipitations occurring in autumn and winter. During the 1950-2023 period, temperatures increased by +0.28°C per decade ($p<0.001$), especially since the early 1980s, while precipitations did not significantly change over time ($p>0.05$). Local climatic conditions most likely vary among the studied stands depending on the elevation (from 9 m to 422 m), distance to the sea, and local topography; however, the spatial resolution of most climate gridded datasets is not accurate enough to capture these variations. In consequence, we could not directly analyze the differences in microclimatic conditions among stands, but rather aimed at capturing them through the consideration of elevation and local topography.

All plots are located within the western part of the Massif des Maures, a crystalline Hercynian massif. The bedrock is metamorphic, dominated by phyllite rocks alternating with quartzite veins (Bordet *et al.,* 1976).

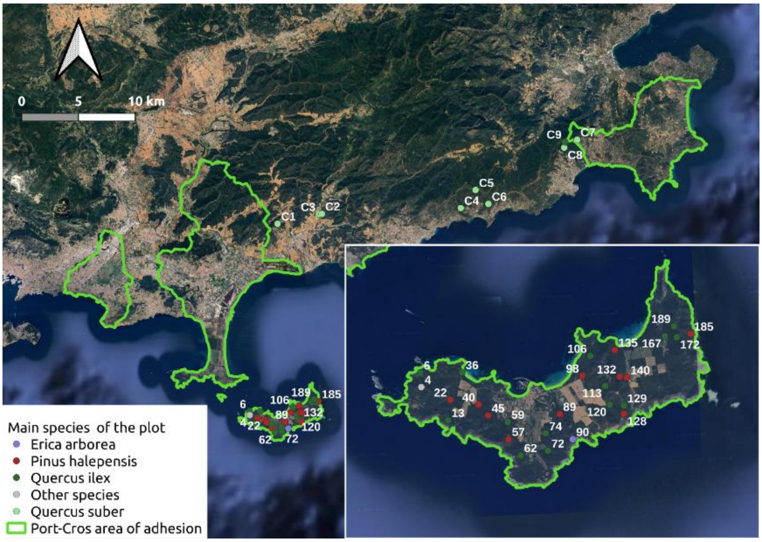

Figure 1. Location of the study plots within the Port-Cros National Park (green lines). The color of the dots indicates the main species in terms of basal area. All plots are identified with a number, they are located on the island of Porquerolles (bottom-right; same plot ID as previous surveys) except nine plots located on the continental part of the park (C1 to C9).

Forest health status and composition

The current health status of the forests of the Port-Cros National Park was evaluated on 400 m^2 plots with homogeneous topographic conditions through two distinct methods involving (i) the quantification of the rate of dead branches and dead trees at plot scale, and (ii) the observation of leaf deficit of the (co-)dominant trees of the plots.

The quantification of tree mortality rate was based on classical dendrometric inventories. Tree diameter at breast height (DBH; at 1.30 m), status (living vs. dead), and species identity were reported for each tree with a DBH ≥ 5 cm within the plot boundaries. This survey also allowed to determine the composition and density of each plot by calculating the number of stems (#/ha) and basal area (m^2/ha) for each species. We also estimated the percentage of dead branches in each vertical stratum of the plot (<0.5 m; 0.5-3 m; 3-6 m; 6-10 m; >10 m), but without differentiating the different species. These percentages were combined into one value per plot by weighting the percentage by the depth of each vertical stratum, the last stratum (>10 m) being extended to maximum canopy height.

In order to estimate leaf deficit, we selected around six dominant or co-dominant trees per plot among the main species *P. halepensis*, *Q. ilex* and *Q. suber* trees, which corresponds to a total of 210 trees (mean = 5.8 trees per plot ; from three to eight depending on the density of adult trees). These trees could be located outside the plot in similar top-edaphic conditions if no dominant tree was present within the 400-m^2 area. Leaf deficit was estimated following the DSF protocol, which serves as the reference standard for France (Goudet *et al.,* 2018), and is similar to the European protocol (Ferretti *et al.,* 2021). Additionally, we measured the dimensions (DBH and height) of these trees, and recorded the potential presence of pests and pathogens.

Site characteristics

In each plot, we estimated the site slope, aspect, and local topography (convex, flat, concave), while site elevation and its topographic situation within the catchment area were derived from the 25 m-resolution Digital Elevation Model from the National Geographic Institute (BD ALTI®). Using these variables, we calculated a radiation index (IKR; Becker and Geremia, 1984), which is the ratio between the mean annual radiation received by the plot and the mean annual radiation that would receive a flat surface corresponding to the horizontal projection of the plot. An IKR value above 1.05 corresponds to a warm exposure, while a value below 0.95 indicates a cool situation. We also computed the topographic index (TPI; Weiss, 2001; see also Lemaire *et al.,* 2022) within a 100 m radius using the QGis open-source software; values above zero indicating a high position on the slope while values close to zero correspond to flat situations or to mid-slopes.

Soil characteristics were estimated directly from a pickaxe-dug trial pit at the center of each plot. The presence of active limestone was estimated at 10 cm depth using 10% hydrochloric acid. Soil texture was estimated at 10 cm depth with the feel method (FAO, 2006), and the total available water (TAW; mm) was calculated based on soil depth, the percentage of coarse elements, and soil texture using the pedotransfer functions developed by Jamagne *et al.* (1977). As soil depth in the trial pit may not be representative of the 400 m^2 plot, it was also estimated using a soil auger at the four corners of each plot. The maximum value of soil depth was then used to compute TAW, as it is best correlated with the health indicators tested here. We finally recorded the traces of human and fire activity (e.g., presence of tree stumps, charcoal, etc.) that could explain part of the variation in forest health not related to the factors mentioned above.

Statistical analyses

We first estimated forest health status using the four indicators described above (tree leaf deficit, branch mortality rate, tree mortality rate in proportion of basal area, and tree mortality rate in proportion of stem number), focusing on the differences among plots and among species. Considering that these health indicators may be inter-correlated, we used a principal component analysis to detect these relationships and decided to further analyze only two response variables: leaf deficit and mortality rate in % of basal area (see Fig. S3).

We then developed two linear, mixed-effect statistical models to detect the main drivers of (1) tree mortality rate and (2) leaf deficit, using the *lme4* package (Bates *et al.,* 2015) of the open-source R software (R Core Team, 2024). These models include all the explanatory variables listed above as fixed effects, i.e., site slope, elevation, TPI, IKR, soil total available water (TAW), stand basal area, stem number, and the proportion of Aleppo pine.

Considering that the number of plots is limited, we did not fit models that predict stand-level mortality rate for each species. Instead, we developed a full model, which includes ‘species’ as random effect to consider that some species show higher mortality rates than others. Note that in this model, we assumed that the different factors affect the mortality rate of each species similarly (no interaction). The response variable was log-transformed to ensure normality of the residuals (using the *LogSt* function from the *DescTools* R package, which specifically designed to account for potential null values in the response variable; Signorell, 2022).

For the models predicting tree leaf deficit, we included tree circumference and height as additional fixed effects, and plot identity as random effect to consider that part of the variability among stands may not be captured by the tested variables. Here, the number of observed trees allowed us to develop a model for *P. halepensis*, and for *Q. ilex* and *Q. suber* together as their leaf deficit distribution was comparable (Fig. 2).

In each case, we selected the best and most parsimonious model, i.e., with the lowest Akaike Information Criterion (AIC). For these models, the significance of the effect of each variable was estimated with the *lmerTest* R package (Kuznetsova *et al.,* 2017). We calculated the marginal and conditional r^2 to depict the variance explained by the fixed effects only (i.e., site, stand, and tree characteristics), and by both fixed and random effects of the model, respectively, using the R package *MuMin* (Bartoń, 2022). In order to assess the part of variance explained by each predictor, we partitioned the variance explained by the fixed effects using the *partR2* R package following Stoffel *et al.* (2021).

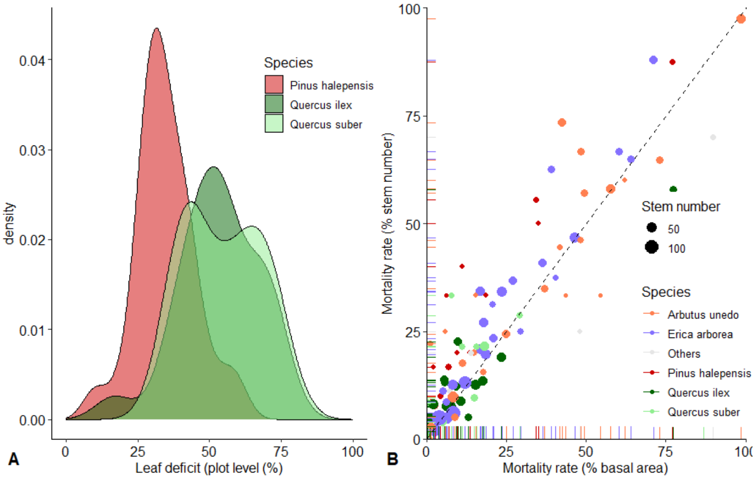

Figure 2. Distribution in plot mean leaf deficit calculated for *Pinus halepensis*, *Quercus ilex*, and *Quercus suber* (A), and relationship between the mortality rates estimated in proportion of stand basal and in proportion of stem number considering all species and study plots (B). The size of the dots indicates the number of stems of the species within the plot. The dots located above the 1:1 line (in dashed) indicate that the mortality mainly affected the trees with a diameter at breast height (DBH) smaller than the mean for this given plot and species.

Results

Main characteristics of the study plots

The study stands are typical of the French Mediterranean forests, with *Pinus halepensis* and oaks (*Quercus ilex* and/or *Quercus suber*) whose composition vary from pure oak forest (e.g., plots C1 to C9 located in the continental part of the PCNP dominated by *Q. suber*) to pure pine forest (e.g., plot 135; Figs. 3 and S2). Stand basal area averages 30.9 m^2/ha with approximately 85 trees per hectare. Even if the shrubs *Arbutus unedo* and *Erica arborea* are highly present in the understory (e.g., plots 90 or C8; see the stem numbers in Fig. S2), they do not strongly contribute to stand basal area (Fig. 3A) due to their small DBH (mean DBH = 7.6 and 6.5 cm, respectively; Table 1). In contrast, *P. halepensis* individuals were quite large (mean DBH = 27.9 cm in the dendrometric survey, the DBH of the (co-)dominant trees reaching a mean of 39.3 cm; Table 1), dominated the upper tree stratum (average height = 13.2 m), while *Q. ilex* and *Q. suber* were in the intermediate tree stratum (average height = 10.7 m and 8.6 m).

There was no active lime in any of the soil profiles, confirming that the soils formed in this area are acidic. They were quite heterogeneous in terms of texture, from heavy clay with 50% clay and 50% silt, to sandy soils with more than 70% of sand. The plot-scale maximum soil depth averaged 58 cm, ranging from 32 to

101 cm. Topographic conditions were contrasted, some plots being located at the hill ridge, while others are in a concave context.

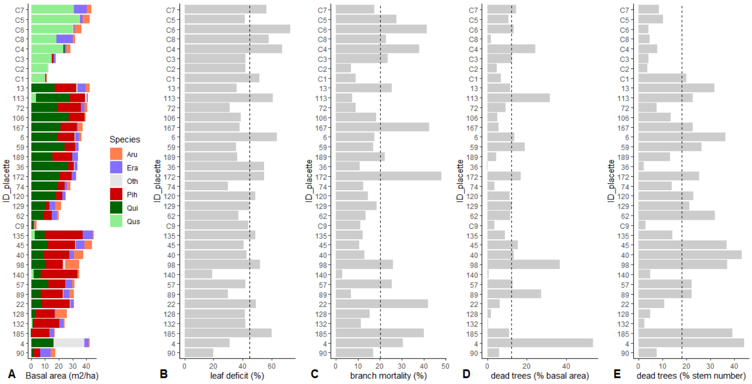

Figure 3. Main characteristics of the study plots in terms of species composition and basal area (A), mean leaf deficit of the dominant trees (B), percentage of dead branches (C) and dead trees (D in % of basal area; E in % of stem number) estimated at plot level. The vertical dashed lines indicate the mean in the different health indicators. The represented shrub species are *Arbutus unedo* (Aru), *Erica arborea* (Era), while the tree species are *Pinus halepensis* (Pih), *Quercus ilex* (Qui) and *Quercus suber* (Qus), while the remaining minor species are included in the group ‘Other’ (Oth). In plot 4, “Other” is mainly composed by planted *Cupressus sempervirens* trees that died recently, which explains the high mortality rates at this plot.

Table 1. Summary characteristics of the density and health status of the main five shrub and tree species recorded in the study. DBH is the tree diameter at breast height.

Species	Number of plots with presence	Dendrometric survey			Leaf deficit assessment			
		Number of individuals with DBH>5 cm	Mean DBH (cm)	Mortality rate (% basal area)	Number of (co-) dominant trees	Mean DBH (cm)	Mean height (m)	Mean leaf deficit (%)
Arbutus unedo	31	563	7.6	26.2				
Erica arborea	32	1225	6.5	17.4				
Pinus halepensis	28	183	27.9	8.8	111	39.3	13.2	35.9
Quercus ilex	29	872	12.5	8.7	66	26.9	10.7	54.0
Quercus suber	12	157	21.8	14.8	33	31.3	8.6	55.6

Forest health status according to different indicators

Most of the study plots and species showed strong signs of forest decline, but the intensity depends on the health indicator used. The leaf deficit of the (co-)dominant trees was generally high, and higher for *Q. ilex* and *Q. suber* (mean at 54.0% and 55.6%, respectively) than for *P. halepensis* (35.9%). Only 13.5% of the *P. halepensis* trees were considered as declining (leaf deficit >=50%), while they represented 68.2% and 63.6% of the observed *Q. ilex* and *Q. suber* trees (Fig. 2A). In consequence, the stands dominated by *Quercus sp.* tended to show higher mean leaf deficit (e.g., plots C2 to C9 in Fig. 3B). Branch mortality rate estimated at the plot level ranged from 3% to 48% with a mean at 20.6%, and showed a similar variation among plots that mean leaf deficit (Fig. 3C). Tree mortality rate was also quite high, averaging 12.4% in terms of basal area, and 18% in terms of stem number. This difference between both indicators reveals that within a plot and for a given species, most of the dead trees are smaller than the average (Fig. 2B). The mortality rates were especially high for *A. unedo* et *E. arborea*; 26.2% and 17.4%, respectively (Table 1).

We also found that some of these health indicators were inter-correlated (Fig. S3). In particular, the proportion of dead trees in terms of basal area was highly correlated with the proportion of dead trees in terms of stem number ($r^2=0.59$; $p<0.001$; Fig. 2B), while the rate of dead branches estimated at plot level was correlated with the leaf deficit of the dominant trees ($r^2=0.40$; $p<0.05$). In consequence, and considering that both groups of variables are independent (Fig. S3), we only analyzed the proportion of dead trees in percentage of basal area, which is less dependent on the health status of the understory (*A. unedo* and *E. arborea*), and on leaf deficit.

Main drivers of forest decline

Based on the mixed-effect models, we found that stand mortality rate was higher in sites with good water supply (concave topography) or water storage (soil with high TAW thanks to a favorable soil texture and/or depth; Table 2). Stands with high basal area, i.e., with higher competition intensity, were also more prone to tree dieback; but note that there was no significant correlation between TAW and stand basal area ($r^2=0.19$; $p>0.1$): the dense stands are not necessarily located on ‘wet’ soils.

Concerning leaf deficit of the (co-)dominant trees, *P. halepensis* trees were more defoliated on sites with warm exposure (i.e., on south-facing steep slopes) and on soils with low water content (Table 2). Similarly, *Quercus* trees tended to show higher leaf deficit on steep slopes. For both taxa, the smallest trees in terms of height (for pine) and DBH (for oaks) were more defoliated. Finally, the opposite relationships between leaf deficit of *Quercus*, stand basal area, and stem number (Table 2) are most likely correlative due to the small number of study plots, and consequently hard to interpret.

All these factors only explained a small percentage of the variance in mortality rate and leaf deficit, as marginal r^2 values ranged from 0.15 to 0.34 (Table 2), and partitioned r^2 values (effect of individual factors) were lower than 0.1. A larger part of the variation in mortality rate among plots was explained by the differences among species (difference between the conditional and marginal r^2 was at 0.24). Similarly, a large part of the variability in leaf deficit was explained at the individual level (e.g., on *Quercus* trees, the marginal r^2=0.15 and the conditional r^2=0.50), but not caused by differences in tree size. Finally, we did not find any relationship between the residuals of these three models and the presence/absence of traces of human and fire activity; and the presence of pests and pathogens was limited and of no effect, only a few *P. halepensis* trees being infested by *Thaumetopoea pityocampa* (processionary moth) and by *Crumenulopsis soraria* (canker on branches).

Table 2. Summary of the selected model for each significant response variable. The sign of the relationship between each factor and the response variable is indicated in parenthesis; the value indicates the partitioned marginal r^2 of each variable, and the asterisks the significance of the effect (*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$). Empty cells indicate non-significant relationships. For local topography, the discrete variables were transformed into numeric ones with “convex”=-1, “flat”=0, and “concave”=1. In consequence, a positive effect indicates that mortality rates are higher in concave situations. IKR is a radiation index whose high values correspond to a warm exposure, TAW the total available water, and DBH the tree diameter at breast height.

Category	Variable	Mortality rate in % of basal area	Leaf deficit *Pinus halepensis*	Leaf deficit *Quercus* spp
Site factors	Local topography	(+) 0.03 **		
	Slope			(+) 0.08 *
	IKR		(+) 0.08 **	
	TAW	(+) 0.03 **	(-) 0.09 *	
Stand factors	Number of trees			(-) 0.06 *
	Basal area	(+) 0.06 **		(+) 0.07 *
Tree characteristics	Tree height		(-) 0.07 ***	
	Tree DBH			(-) 0.04 *
	Nb observations	149	111	99
	Marginal r^2	0.17	0.34	0.15
	Conditional r^2	0.41	0.54	0.50

Discussion

The overview of the forest health carried out in 2023 in the Port-Cros National Park revealed high tree mortality rates and leaf deficit, suggesting that they were mainly in a declining state.

Specifically, 68.2% of the *Quercus ilex* and 63.6% of the *Quercus suber* trees, were classified as declining, with a leaf deficit ≥ 50%. For *Q. suber*, the value exceeds the regional average (51% decline), as reported by the DSF in South-Eastern France (DSF, 2024). For *Q. ilex* the comparison with the last estimates (41% of the trees were declining in 2019; Bec *et al.,* 2020) is challenging considering the gradual increase in leaf deficit over the last years (GREC-SUD, 2024). Nevertheless, it appears that the health status of the (co-)dominant *Quercus* trees in the Port-Cros National Park is worse than the regional average.

In contrast, only 13.5% of the *P. halepensis* trees were classified as declining; and the mean leaf deficit was at 35.9%, which is lower than the regional average (~42%; GREC-SUD, 2024) and values reported in other regions (e.g., 52% in the ‘Bassin Minier de Provence’ located between Marseille and Aix-en-Provence; Ostle, 2023). The percentage of dead trees and shrubs was 12.4% in terms of basal area, and 18% in terms of stem number, but lower when focusing on the species of the overstorey (*P. halepensis*, *Q. ilex* and *Q. suber*; mean at 10.8% in terms of basal area) than on the shrubs of the understorey (*A. unedo* and *E. arborea*; mean at 21.8%). Still, these rates were high when compared with the 5% reported for the entire France (in terms of volume; IGN, 2024). This discrepancy cannot be attributed to our sampling strategy, as the plots were chosen to encompass a wide range of environmental conditions, including topography, soil, and stand characteristics, without prior knowledge of tree mortality rates.

We were unable to quantify the proportion of variability in forest health attributable to climatic conditions (see Materials and Methods), and the models showed no effect of stand elevation. However, it seems obvious that overall, drought was the main driver of forest decline in the Port-Cros National Park. While rainfall remained relatively stable from 1950 to 2023, temperatures rose significantly (Fig. S1), increasing the evaporative demand, and intensifying drought stress on the vegetation (e.g., Park Williams *et al.,* 2013). This warming trend since the late 1980s aligns with the increase in leaf deficit rate observed in various species in the French Mediterranean region (DSF, 2024; GREC-SUD, 2024). In addition, the particularly dry years of 2017 and 2020 (with less than 360 mm of rainfall; i.e., < 58% of the mean), likely exacerbated the decline process. Similar studies carried out in South-Eastern France also emphasized the key role of drought in the decline of the

Mediterranean tree species (Lemaire *et al.,* 2022 for *P. sylvestris*; Bec *et al.,* 2020 for *Q. ilex*).

In this regard, there is an apparent contradiction in the effect of site characteristics on leaf deficit and tree mortality rate. On the one hand, the (co-)dominant trees surveyed in the PCNP showed more severe leaf deficits in drier and/or warmer site conditions, particularly in areas with unfavorable topography (steep slope, south-facing aspect), or poor water-retention soils (sandy or shallow soil). On the other hand, higher tree mortality rates were observed in sites with good water supply or storage. The first result seems obvious, is commonly observed (e.g., Galiano *et al.,* 2010; Lemaire *et al.,* 2022) and suggest that drought effects can be exacerbated when sites conditions are unfavorable. The second result has also been obtained elsewhere (e.g., Socha *et al.,* 2023) and suggest a lack of acclimation of trees to dry conditions. In such ‘wet’ environments, trees often prioritize leaf and branch growth over the development of the rooting system (phenomenon known as “structural overshoot”), leaving them vulnerable when climatic conditions become drier (Jump *et al.,* 2017). This apparent contraction confirms that leaf deficit and tree mortality are not the same stages of forest decline (leaf-shedding can signal the early stages of a sequence leading to tree death; Galiano *et al.,* 2010), and may be caused by species-specific differences in responses to drought; effects that are difficult to unravel here due to the small number of plots sampled.

Beyond drought, we could show that stand densification and canopy closing also contributed to decline. A progressive dynamics of *Q. ilex* forest to the detriment of high scrubland has been reported by Lavagne *et al.* (2007) from 1979 to 2004; and our study suggests that this process is still ongoing. The stands are undergoing a self-thinning process, a natural stage in forest succession as stands transition from young to mature forests. This is demonstrated by the facts that (i) stands with high basal area showed higher mortality rates; (ii) the smallest trees showed the highest leaf deficit and mortality rates; (iii) the shrubs *A. unedo* and *E. arborea* with lower longevity and shade tolerance were more prone to die. Interestingly, the presence of pests and pathogens was notably low; with no evident signs of black-banded oak borer [*Coroebus florentinus* (Herbst, 1801)], a pest commonly found in South of France (Bec *et al.,* 2020).

We acknowledge that our statistical models did not capture most of the variation in leaf deficit and tree mortality rates among sites, as indicated by the low r^2 values. This is mainly due to the heterogeneity in environmental conditions that occur within a plot (e.g., variations in soil and in competition experienced by each tree), and to the complexity to accurately assess soil total available water with conventional pedological methods (e.g., tree roots go deeper than the pit bottom). In addition, even though we took care to sample plots in contrasted environments, the limited sample size of trees and plots restricts the ability to obtain robust results that can be extrapolated at broader scale. In consequence, this descriptive and comprehensive overview should be expanded using a larger sampling and in similar regions, to better understand the high stand mortality and high leaf deficit rates in *Quercus* species in the Port-Cros National Park. In addition to differences in soil and climatic conditions in comparison to other regions from South-Eastern France, another explanation would be the absence of forest management and of sanitary thinning in the PCNP, which automatically increase the presence of dead trees in the field.

Finally, our study suggests that the absence of forest management in Mediterranean areas can lead to contrasting effects. On the one hand, dense stands are more prone to tree and shrub dieback, may accumulate living and dead fuel loads, which consequently increases fire risk in these areas. On the other hand, certain components of biodiversity linked to mature stages are enhanced such as the fauna and fungi associated with deadwood and tree-related microhabitats. This calls for a further exploration of the potential impacts of climate change and management on forest decline and the resulting change in ecosystem services (Moran-Ordonez *et al.,* 2021), but also for special measures to reduce fire risk, spread and potential impacts (e.g., landscape management; Fernandes, 2013).

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References

ALLEN C.D., BRESHEARS D.D., McDOWELL N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6 (8): 1-55.

BARTOŃ K., 2024 MuMIn: Multi-Model Inference. R package version 1.48.4, https://CRAN.R-project.org/package=MuMIn

BATES D., MAECHLER M., BOLKER B., WALKER S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.*, 67 (1): 1–48.

BEC R., DAUBRÉE J.B., CAILLERET M., VENNETIER M., 2020. État des lieux du dépérissement de chêne vert en région méditerranéenne. *Forêt Entreprise*, 251 : 36-40.

BECKER M., GEREMIA F., 1984. Indices de climat lumineux selon la pente et l'exposition pour les latitudes de 40 à 50. *Bull. Écol.,* Paris, 15 (4) : 239-252.

BORDET P., BLANC J., JEUDY de GRISSAC A., CHAMLEY H., DUROZOY G., 1976. Hyères-Porquerolles, carte géologique de la France au 1:50.000. *Bur. Rech. Géol.Min. (BRGM): Paris*, 34 : 21-383.

CARNICER J., COLL M., NINYEROLA M., PONS X., SANCHEZ G., PENUELAS J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl. Acad. Sci.*, 108 (4): 1474-1478.

DSF, 2023. Indicateurs de santé des forêts (1989-2022), Rapport 3p. https://agriculture.gouv.fr/telecharger/136245.

DSF, 2024. Indicateurs de l'état de santé des forêts pour les régions du pôle Sud Est - Année 2023. https://draaf.paca.agriculture.gouv.fr/indicateurs-de-l-etat-de-sante-des-forets-du-pole-sud-est-a4023.html.

FAO, 2006. *Guidelines for soil description*. Food & Agriculture Organization, Rome, Italy.

FERNANDES, P. M., 2013. Fire-smart management of forest landscapes in the Mediterranean basin under global change. *Landsc. Urb. Plann.*, 110: 175-182.

FERRETTI M., BACARO G., BRUNIALTI G., CALDERISI M., CROISÉ L., FRATI L., NICOLAS M., 2021. Tree canopy defoliation can reveal growth decline in mid-latitude temperate forests. *Ecol. Indic.*, 127: 107749.

GALIANO L., MARTINEZ-VILALTA J., LLORET F., 2010. Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems*, 13: 978-991.

GALVÁN J.D., CAMARERO J.J., GINZLER C., BÜNTGEN U., 2014. Spatial diversity of recent trends in Mediterranean tree growth. *Environ. Res. Lett.*, 9 (8), 084001.

GAUQUELIN T., MICHON G., JOFFRE R., DUPONNOIS R., GENIN D., FADY B., BOU DAGHER-KHARRAT M., DERRIDJ A., SLIMANI S., BADRI W., 2018. Mediterranean forests, land use and climate change: a social-ecological perspective. *Reg. Envir. Change*, 18: 623-636.

GOUDET M., SAINTONGE F.-X., NAGELEISEN L.-M., 2018. *Quantifier l'état de santé de la forêt, méthode simplifiée d'évaluation*. 6 pp. https://agriculture.gouv.fr/telecharger/90879.

GREC-SUD, 2024. La pollution atmosphérique à l'ozone et le changement climatique en région Provence-Alpes-Côte d'Azur. Les cahiers du GREC-SUD, édités par l'Association pour l'innovation et la recherche au service du climat (AIR Climat): 40 pp.

GUIOT J., CRAMER W., 2016. Climate change: The 2015 Paris Agreement thresholds and Mediterranean basin ecosystems. *Science*, 354 (6311): 465-468.

IGN, 2024. Inventaire Forestier National, Mémento 2024, 72pp. https://www.ign.fr/publications-de-l-ign/institut/kiosque/publications/docs_thematiques/memento-2024.pdf.

JAMAGNE M., BÉTRÉMIEUX R., BÉGON J.C., MORI A., 1977. Quelques données sur la variabilité dans le milieu naturel de la réserve en eau des sols. *Bull. Techn. Inform.*, 324 : 627-641.

JUMP A.S., RUIZ-BENITO P., GREENWOOD S., ALLEN C.D., KITZBERGER T., FENSHAM R., MARTÍNEZ-VILALTA J. LLORET, F., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Glob. Change Biol.*, 23 (9): 3742-3757.

KUZNETSOVA A., BROCKHOFF P.B., CHRISTENSEN R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. *J. Stat. Softw.*, 82 (13): 1-26.

LAVAGNE A., BIGEARD N., DELAYE F., MASOTTI V., 2007. Étude de la dynamique forestière de l'île de Port-Cros (Parc national de Port-Cros, Var, SE France) de 1968 à 2004. *Sci. Rep. Port-Cros Natl. Park*, 22: 195-232.

LEMAIRE J., VENNETIER M., PREVOSTO B., CAILLERET M., 2022. Interactive effects of abiotic factors and biotic agents on Scots pine dieback: A multivariate modeling approach in southeast France. *For. Ecol. Manag.*, 526, 120543.

MORÁN ORDÓÑEZ A., RAMSAUER J., COLL L., BROTONS L., AMEZTEGUI A., 2021. Ecosystem services provision by Mediterranean forests will be compromised above 2℃ warming. *Glob. Change Biol.*, 27 (18): 4210-4222.

NEUMANN M., MUES V., MORENO A., HASENAUER H., SEIDL R., 2017. Climate variability drives recent tree mortality in Europe. *Glob. Change Biol.*, 23(11): 4788-4797.

OSTLE M., 2023. *Determining the factors associated with Pinus halepensis forest decline in the Provence Mining Basin (BMP), France*. MSc thesis. Sorbonne Université.

PARK WILLIAMS A., ALLEN C.D., MACALADY A.K., GRIFFIN D., WOODHOUSE C.A., MEKO D.M., SWETNAM T.W., RAUSCHER S.A., SEAGER R., GRISSINO-MAYER H.D., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change*, 3 (3): 292-297.

QUÉZEL P., MÉDAIL F., 2003. Que faut-il entendre par" forêts méditerranéennes"?. *Forêt Méditerranéenne*, 24 (1) : 11-31.

R CORE TEAM, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

SARRIS D., CHRISTODOULAKIS D., KÖRNER C., 2007. Recent decline in precipitation and tree growth in the eastern Mediterranean. *Glob. Change Biol.*, 13 (6): 1187-1200.

SIGNORELL, 2022. DescTools: Tools for descriptive statistics (manual).

SOCHA J., HAWRYŁO P., TYMIŃSKA-CZABAŃSKA L., REINEKING B., LINDNER M., NETZEL P., GRABSKA-SZWAGRZYK E., VALLEJOS R., REYER, C.P., 2023. Higher site productivity and stand age enhance forest susceptibility to drought-induced mortality. *Agric. For. Meteorol.*, 341, 109680.

SONG J., ZHOU S., YU B., LI Y., LIU Y., YAO Y., WANG S. FU B., 2024. Serious underestimation of reduced carbon uptake due to vegetation compound droughts. *npj Clim. Atm. Sci.*, 7 (1): 23.

STOFFEL M.A., NAKAGAWA S., SCHIELZETH H., 2021. partR2: Partitioning R2 in generalized linear mixed models. PeerJ 9:e11414

TACCOEN A., PIEDALLU C., SEYNAVE I., GÉGOUT-PETIT A., GÉGOUT J.C., 2022. Climate change-induced background tree mortality is exacerbated towards the warm limits of the species ranges. *Ann. For. Sci.*, 79 (1), 23.

WALKER A.P., DE KAUWE M.G., BASTOS A., BELMECHERI S., GEORGIOU K., KEELING R.F., McMAHON S.M., MEDLYN B.E., MOORE D.L.P. RICHARD J. NORBY R.J., *et al*. 2021. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO_2. *New Phytologist*, 229 (5): 2413-2445.

WEISS A., 2001. Topographic position and landforms analysis. In *Poster presentation, ESRI user conference, San Diego, CA* (Vol. 200).

Annexes

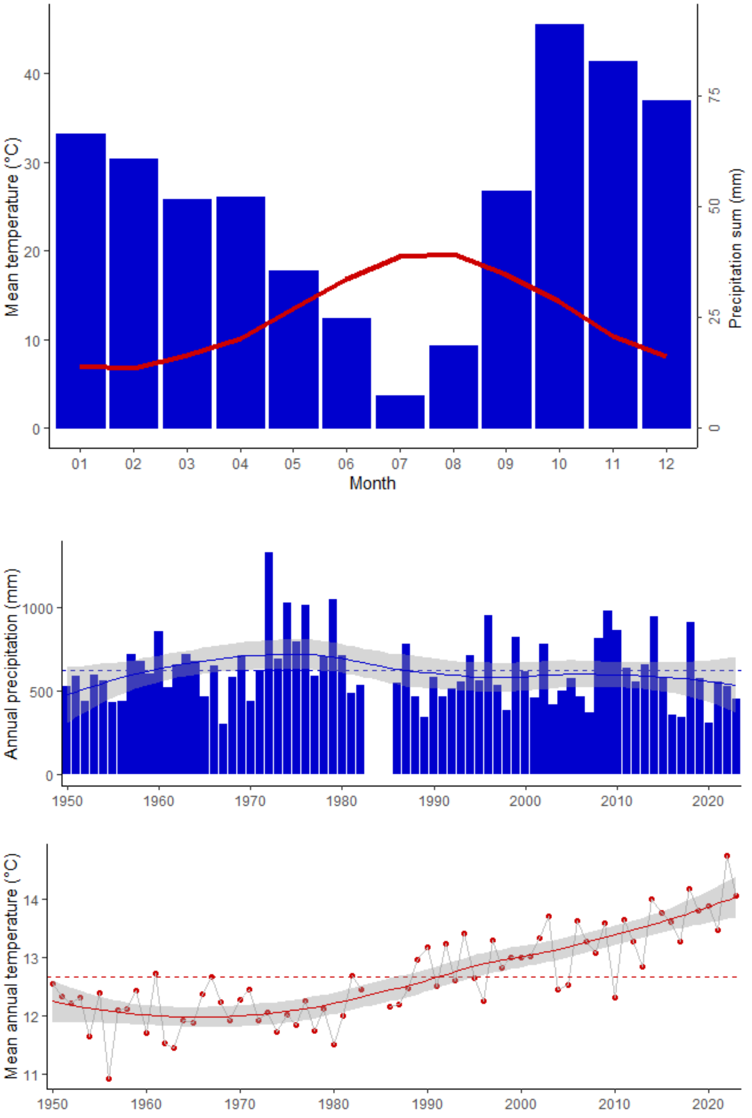

Figure S1. Climate diagram (Left) and temporal change in annual precipitation (blue bars) and mean annual temperature (red dots) from 1950 to 2023. Data from Meteo-France, weather station of Porquerolles. Some monthly values are missing in the Meteo-France database in 1983, 1984, 1985, which explained the interruptions in the time-series. Dashed lines indicated the mean values, while smoothing splines highlighted the temporal trends (loess method).

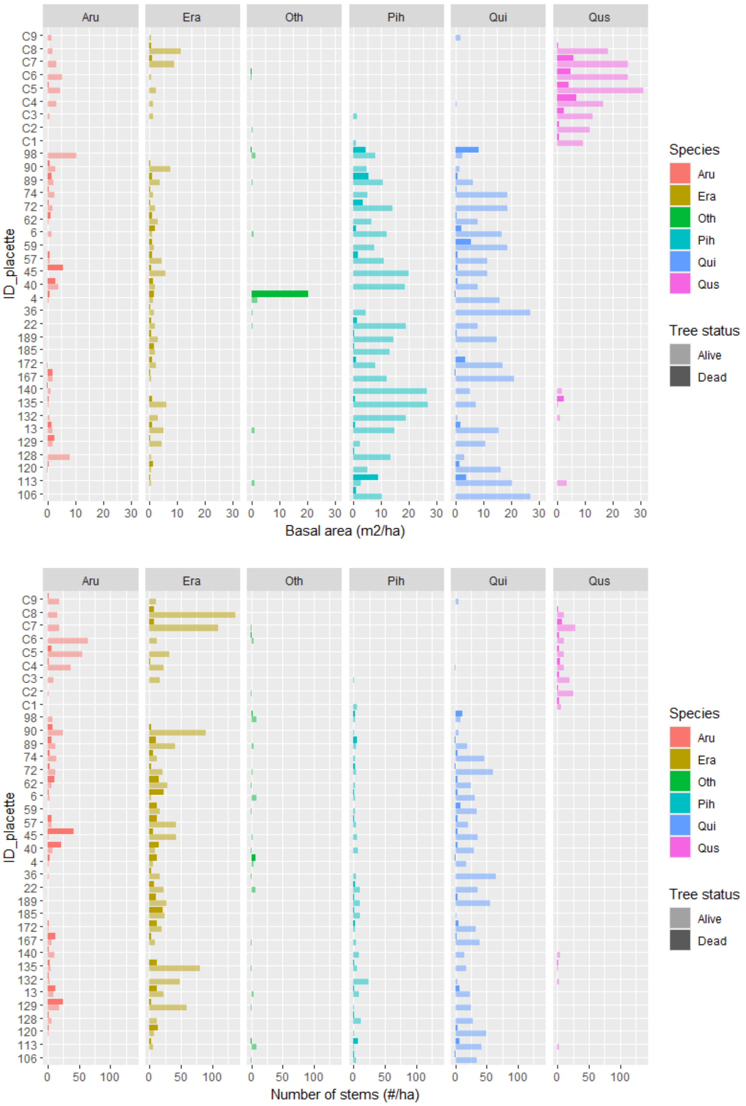

Figure S2. Main characteristics of the study plots in terms of species basal area (top) and number of stems (bottom), according to tree health status: living (dark colors) vs. dead (light color). The represented tree species are *Arbutus unedo* (Aru), *Erica arborea* (Era), *Pinus halepensis* (Pih), *Quercus ilex* (Qui) and *Quercus suber* (Qus), while the remaining minor species are included in the group 'Other' (Oth).

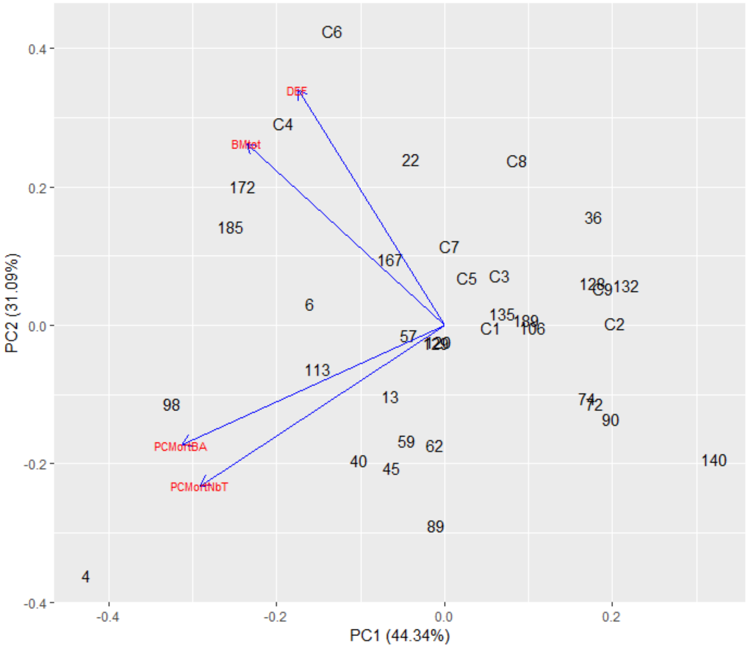

Figure S3: Principal component analysis showing the relationships between the different health indicators (DEF: leaf deficit; BMtot: percentage of dead branches; PCmortBA: tree mortality rate in percentage of basal area; PCMortNbT: tree mortality rate in percentage of stem number), and the location of the plots (see Fig. 1) within this multivariate space.