

Mistletoe negatively impacts vigor, growth and reproduction of silver fir forests at regional and local scales

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ARTICLE INFO

Keywords:

Abies alba
Cone production
Crown defoliation
Dendroecology
Pyrenees
Viscum album

ABSTRACT

Mistletoes impact their tree hosts in different ways and affect distinct processes such as growth and reproduction. However, comparative assessments of mistletoe effects on these two processes are scarce, particularly at different spatial scales. Here, we quantified how mistletoe (*Viscum album* L.) affected radial growth and cone production of silver fir (*Abies alba* Mill.), a major European conifer. We assessed these impacts at continental (2004–2019 period, 301 plots across Europe), regional (western Spanish Pyrenees, 0.5° W–0.5° E and 42.5°–43.0° N, 30 sites and 360 trees) and local scales (two Pyrenean stands with severe mistletoe infestation – VI and SN sites). Mistletoe abundance enhanced crown defoliation at all scales. At continental scale, the percentage of infested trees has been increasing reaching values close to 15 % in 2019. At regional scale, mistletoe infestation was severe in 19 % of sampled trees. At local scale, mistletoe infestation contributed to forest decline through growth loss and decreased cone production. Silver fir stands with more trees heavily infested by mistletoe showed abundant winter fleshy-fruited species such as *Sorbus aria*. Mistletoe led to lasting (12 years prior to sampling) and irreversible growth reduction (–78 % in site VI, –44 % in site SN) in severely infested trees as compared to lightly infested coexisting trees. The acute defoliation of the upper crown in severely infested trees negatively impacted cone production, but this effect was significant only at local scale. Thus, continental-wide assessments of mistletoe infestation and how it impacts defoliation, growth and cone production should be carefully validated and refined by regional and local data.

1. Introduction

Forest die-off and growth decline, often preceding severe mortality events, have been described in forests around the world (Senf et al., 2025). Such episodic events have been attributed to hotter droughts (Hammond et al., 2022), but their severity could be intensified by the increasing incidence of biotic stressors including insects, pathogens and hemiparasitic plants (e.g., Sangüesa-Barreda et al., 2015; Das et al., 2016). Obligate hemiparasitic aerial plants such as mistletoes contribute to growth decline and dieback, particularly in seasonally dry areas where they amplify drought stress, and their distribution area could expand due to climate warming and forest encroachment (Sangüesa-Barreda et al., 2018; Walas et al., 2022). Mistletoes can exacerbate drought damage on trees by causing hydraulic dysfunction of defoliated and infested trees and placing them at higher risk of hydraulic

failure (Fischer, 1983; Glatzel and Geils, 2009; Zweifel et al., 2012; Griebel et al., 2022). European mistletoes have been considered relevant contributors to canopy dieback and tree mortality in several conifer species including pines (*Viscum album* subsp. *austriacum* (Wiesb.) Vollmann; Dobbervin and Rigling, 2006; Rigling et al., 2010; Sangüesa-Barreda et al., 2012, 2013) and firs (*Viscum album* subsp. *abietis* (Wiesb.) – we refer to this subspecies as *Viscum album* for simplicity; Tsopelas et al., 2004; Raftoyannis et al., 2015; González de Andrés et al., 2024a). Nevertheless, mistletoes and their hosts can co-exist for years without apparent symptoms of vigor loss in the host tree in the absence of resource limitations (Zuber, 2004). Therefore, retrospective data on mistletoe impacts on tree growth are required to understand how the host trees are affected in the long term (e.g., Camarero et al., 2019).

Mistletoes negatively impact several performance components of host trees (Mathiasen et al., 2008; Thomas et al., 2023). Mistletoes are

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<https://doi.org/10.1016/j.foreco.2025.122693>

Received 12 February 2025; Received in revised form 22 March 2025; Accepted 24 March 2025

Available online 30 March 2025

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xylem-tapping plants which tend to show higher water-use efficiency than host trees, and uptake some nutrients (e.g., P, K) from host tissues (Mutlu et al., 2016; González de Andrés et al., 2024a; Zhang et al., 2023, 2024). In general, mistletoe infestation causes abundant leaf shedding (crown defoliation), triggers radial growth decline and contributes to tree death (Dobbertin and Rigling, 2006; Kollas et al., 2018; Camarero et al., 2019). For instance, mistletoes reduce leaf size, leaf nutrient content, leaf chlorophylls content, carbon assimilation and growth rates leading to a loss of vitality and apical die-off in several of its main host tree species such as Scots pine (*Pinus sylvestris* L.) or silver fir (*Abies alba* Mill.) (Yan et al., 2016; Bilgili et al., 2018; Ozturk et al., 2019, 2022; González de Andrés et al., 2024a). In these two major conifer species, severe mistletoe infestation prompts abundant and premature needle shedding and branch dieback, particularly in the upper crown where hydraulic limitations are observed (Fischer, 1983; Rigling et al., 2010; Barbu, 2009, 2012; Zweifel et al., 2012). Mistletoe-triggered growth decline often accompanies crown defoliation and leads to impaired vitality in conifers (Noetzi et al., 2003; Tsopelas et al., 2004; Dobbertin and Rigling, 2006; Sangüesa-Barreda et al., 2012, 2013; Raftoyannis et al., 2015; Mellado and Zamora, 2017). This explains why mistletoe removal experiments have resulted in increased N and non-structural carbohydrate concentrations and improved growth rates of the hosts as compared with infested trees (Yan et al., 2016; González de Andrés et al., 2024b).

In addition to the loss in growth and vigor, severe mistletoe infestation reduces flowering and fruiting resulting in small crops as was found in affected apple (*Malus domestica* Borkh.) trees (Preston, 1977). Interestingly, hemiparasitism can cause a decline in the reproductive output (e.g., crop size) without conspicuous loss of growth. For example, mistletoe infestation impaired the reproductive capacity of Scots pine, leading to fewer cones per tree, less seed production, smaller seeds and lower germination and emergence success, with small impacts on growth (Mellado and Zamora, 2019). However, our knowledge on how mistletoe impacts tree reproduction and growth is still limited. Thus, cone or seed production assessments of infested trees should be more widely studied and compared with long-term impacts on radial growth. Mistletoe infestation can be critical for silver fir which produces most of its cones in the uppermost crown (Dobrowolska et al., 2017), where mistletoe impacts are severe (Sangüesa-Barreda et al., 2012). Moreover, warmer temperatures can amplify drought stress decreasing host performance and promoting defoliation (Sangüesa-Barreda et al., 2018).

Here, we analysed how silver fir defoliation, growth, cone and seed production were affected by European mistletoe at three spatial scales: continental (Europe), regional (Spanish Pyrenees) and local (two Pyrenean sites with high infestation degree). Mistletoe infestation has been considered an important contributing factor of recent dieback in some Pyrenean silver fir stands located near the South Western distribution limit of the species in Europe (Oliva and Colinas, 2007, 2010; Camarero et al., 2011). There, stands with a higher number of mistletoe-infested trees showed greater defoliation and higher mortality rates (Gazol et al., 2020). We aimed to assess mistletoe impacts on growth and reproduction of silver fir using data from European ICP-Forest level I plots (Michel et al., 2020), and field-based information comprising regional data from the Spanish Pyrenees and local data from two severely infested stands. We hypothesized that severe mistletoe infestation negatively impacted silver fir growth and cone production through enhanced crown defoliation, a proxy of tree vigor loss.

2. Materials and methods

2.1. Data on mistletoe occurrence in European silver fir forests

At continental scale, mistletoe occurrences in European silver fir stands were obtained from the ICP Forests Level 1 forest health survey. The ICP Forest collaborative project started in the early 1980s and conducts annual assessments of tree condition at a 16 km grid (Fig. S1)

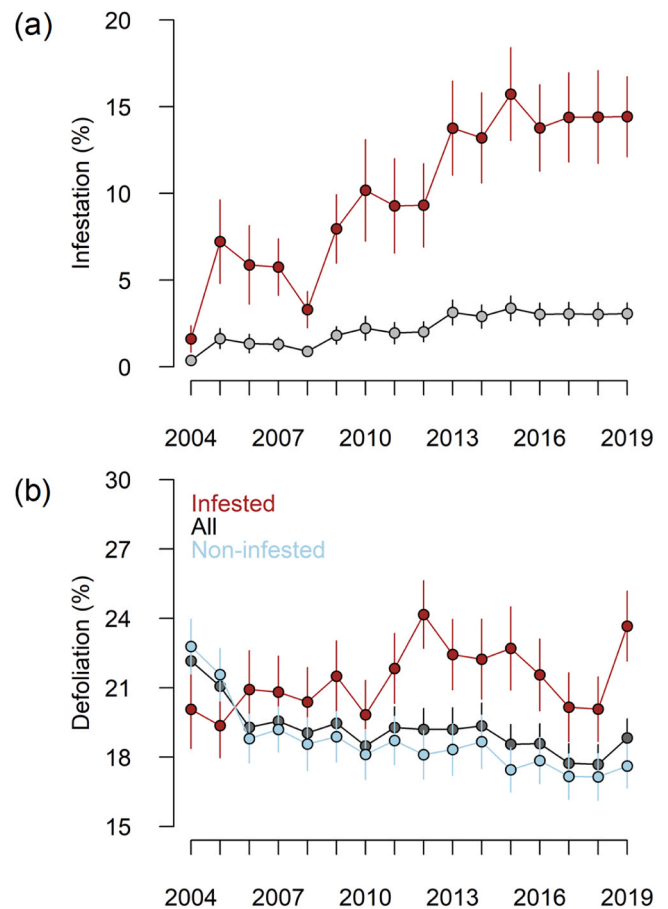


Fig. 1. Trends in the percentage of trees showing (a) mistletoe infestation for all monitored plots (grey symbols) and for plots with mistletoe presence (brown symbols). (b) Changes in crown defoliation of all monitored plots, plots with mistletoe infestation and plots without mistletoe (blue symbols). Analyses were based on ICP-forest network data, period 2004–2019.

across the continent using harmonized methods (Eichhorn et al., 2016; Michel et al., 2020). In each plot, a varying number of trees (typically 20) at least 0.6 m high are surveyed every year to quantify, among other variables, defoliation percentage and to identify damaging agents, i.e. abiotic or biotic stressors (Eichhorn et al., 2016).

First, we selected the occurrence of silver fir trees in the Crown condition parameters Level I (Visual Assessment of Crown Condition) and related this to the Damage parameters Level I. After removing duplicates, we obtained a total of 301 plots dominated by silver fir which were monitored from 2004 to 2019 (Fig. 1 and S1). In those plots, 3447 silver fir trees were measured. We identified the presence of mistletoe in the trees according to the Damage parameters Level I table by identifying “*Viscum album*” as a damage cause. The extent of the damage was recorded in an 8-point scale with 0 being the lowest value and 7 representing 100 % damage. The total number of mistletoe occurrence was 1343 (trees x year) corresponding to 300 trees. Out of the 1343 occurrences, 119 had a value of 0, 647 had a value of 1, 321 of 2, 211 of 3 and only 45 values ranged 4–7 (33). For the selected trees, we also retained the assessment of cone production which is visually assessed. Giving that this variable (coning index) is recorded in a scale from 0 (absent) to 3 (high) we only considered whether cones were absent (0) or not (> 0).

2.2. Data on mistletoe infestation level at regional scale

At regional scale, we selected 23 silver fir stands (Fig. 2, Table 1) in the central and western Spanish Pyrenees (Aragón region), where the research team monitored the vigor and growth of these populations in

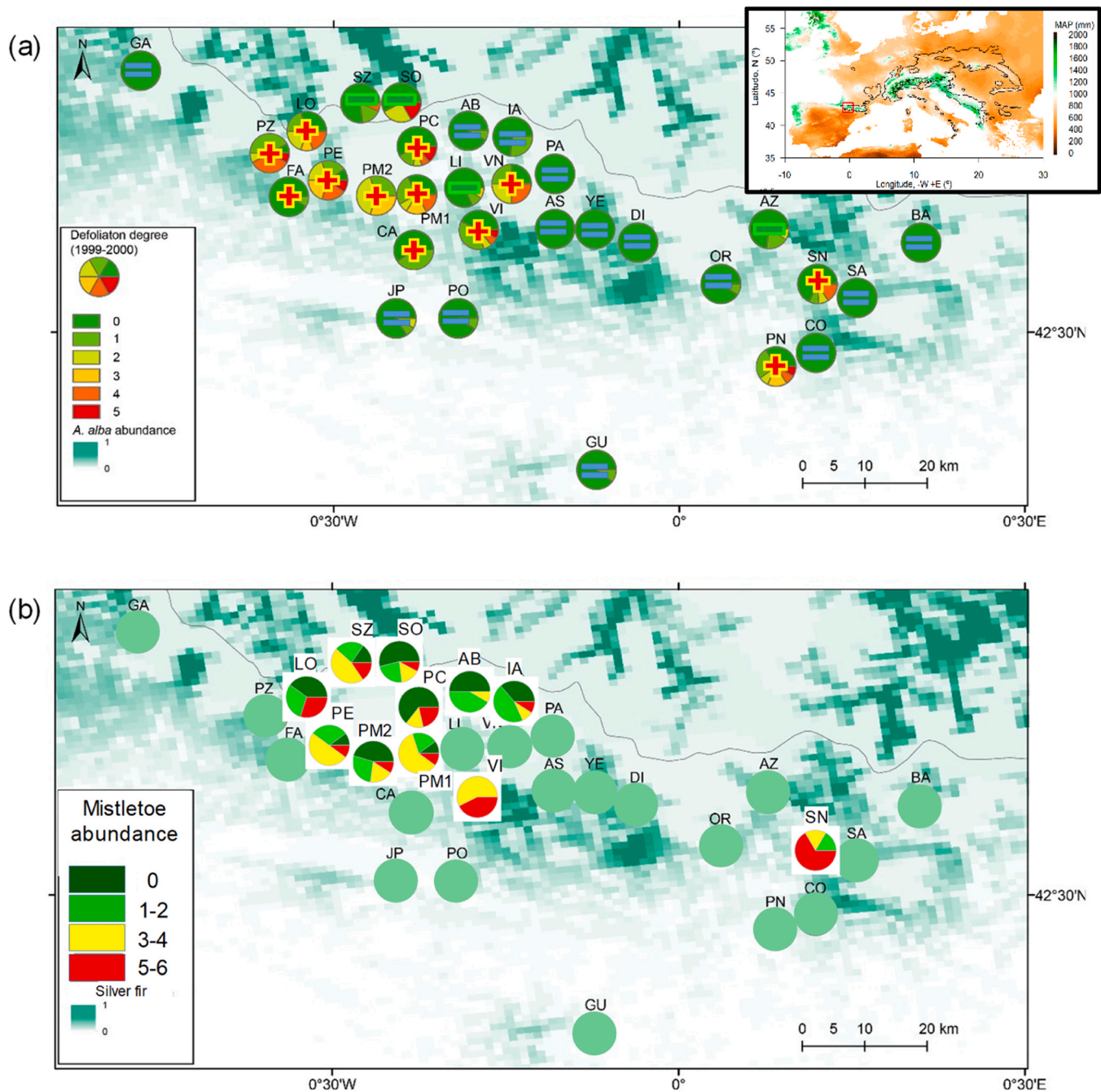


Fig. 2. Maps showing (a) crown defoliation levels of western Pyrenean silver fir stands and changes from 1999–2000 to 2023 (+, increase; –, reduction; =, similar levels). Data correspond to 1999–2000 and symbols correspond to 2023. (b) Mistletoe abundance in the stands with mistletoe presence (data correspond to 1999–2000). In both maps, the green background shows silver fir abundance. Local scale assessments were conducted in sites VI and SN (see Table 1). The upper inset in plot (a) shows the silver fir distribution in Europe (black lines), the location of the study region (red box), and total annual precipitation (MAP, color background).

1999–2000 and 2020–2023 (Camarero et al., 2011; Gazol et al., 2020; Crespo-Antia et al., 2024). In each stand, mature silver firs were selected and measured along 100-m long and 10-m wide transects. We measured the diameter at 1.3 m (dbh, diameter at breast height), the defoliation and mistletoe infestation levels of 20–44 trees per stand. We also estimated the stand basal area of silver fir and the second most abundant tree species (European beech, *Fagus sylvatica* L.). Crown defoliation was visually assessed (0–100 %) and percentages were converted into a semi-quantitative scale ranging from 0 (no or scarce defoliation) to 5 (fully defoliated, dead tree). Very defoliated or declining trees were considered those showing defoliation level > 3. Therefore, the

percentage of defoliation of the stand was calculated as the proportion of trees with crown defoliation level > 3. We used the Hawksworth (1977) six-class rating system to assess mistletoe infestation levels of trees sampled in the field. They were estimated by dividing the tree crown in three similar vertical sectors and each third was classified as 0 (absence of mistletoe), 1 (light to moderate mistletoe infestation) or 2 (severe mistletoe infestation). Then, the mistletoe infestation degree of each tree was obtained summing the rates of each crown third. The infestation levels ranged 0–6 and we considered as very infested trees those showing a mistletoe infestation degree ≥ 3 and presenting values > 1 in the uppermost crown. Finally, cone production was also estimated using

Table 1

Characteristics of the studied Pyrenean silver fir stands. Underlined sites' names correspond to those sites with severe mistletoe infestation where local assessments were carried out.

Site (code)	Latitude (°N)	Longitude (°, –W, +E)	Elevation (m a.s.l.)	Diameter at 1.3 m (cm)	Basal area of silver fir (m ² ha ⁻¹)	Defoliated trees (%)	Mistletoe (% trees with degree ≥ 3)
Fago (FA)	42.725	–0.876	931	61.3 ± 1.6	45.9	5.0	0.0
Paco Ezpela (PE)-high	42.741	–0.830	1232	27.8 ± 0.4	21.7	26.3	4.5
Paco Ezpela (PZ)-low	42.741	–0.829	1080	24.3 ± 0.2	20.4	29.6	0.0
Lopetón (LO)	42.770	–0.827	1009	38.1 ± 2.7	24.8	20.0	18.0
Gamueta (GA)	42.885	–0.796	1395	56.3 ± 3.7	56.2	2.0	0.0
Selva de Oza–2 (SZ)	42.830	–0.720	1272	58.2 ± 3.1	38.3	9.0	15.4
Selva de Oza–1 (SO)	42.830	–0.716	1195	35.7 ± 1.3	34.0	5.0	7.7
S. Juan de la Peña (JP)	42.505	–0.690	1393	29.0 ± 0.6	12.4	0.0	0.0
Paco Mayor–1 (PM1)	42.700	–0.640	1353	43.5 ± 0.5	22.0	24.1	0.0
Paco Mayor–2 (PM2)	42.750	–0.635	1313	54.8 ± 5.1	34.2	25.0	11.1
Puente de Corralones (PC)	42.767	–0.630	1248	47.5 ± 3.0	43.3	14.0	21.4
Lierde (LI)	42.691	–0.545	1222	59.2 ± 2.2	109.2	9.1	0.0
Peña Oroel (PO)	42.520	–0.537	1604	29.0 ± 0.6	47.9	18.2	0.0
Los Abetazos (AB)	42.720	–0.533	1403	75.0 ± 4.4	63.8	0.0	4.0
Castiello de Jaca (CA)	42.639	–0.531	1175	39.4 ± 1.7	71.6	23.7	0.0
Izquierda del Aragón (IA)	42.750	–0.530	1478	69.0 ± 5.6	56.0	0.0	9.1
Paco de Villanúa (VN)-high	42.680	–0.505	1320	38.4 ± 1.2	24.2	5.0	0.0
<u>Paco de Villanúa (VI)-low</u>	42.680	–0.501	1235	42.5 ± 0.9	48.0	18.2	28.6
Paco Asieso (AS)	42.650	–0.300	1327	60.6 ± 3.6	37.2	0.0	0.0
Yésero (YE)	42.650	–0.220	1399	48.1 ± 3.1	31.7	5.0	0.0
Guara (GU)	42.300	–0.200	1428	52.5 ± 2.6	13.5	0.0	0.0
Diazas (DI)	42.630	–0.080	1528	31.4 ± 0.5	53.4	0.0	0.0
Orús (OR)	42.567	0.080	1370	42.3 ± 1.5	39.5	0.0	0.0
Azitrón (AZ)	42.650	0.217	1613	48.0 ± 3.6	33.3	0.0	0.0
Peña Montañesa (PN)	42.450	0.230	1519	45.1 ± 2.2	28.5	12.0	0.0
Collubert (CO)	42.467	0.300	1474	51.0 ± 4.4	29.6	0.0	0.0
<u>Selva Negra (SN)</u>	42.567	0.333	1431	49.5 ± 3.5	29.1	16.0	66.7
Sahún (SA)	42.550	0.383	1789	50.1 ± 2.8	36.6	0.0	0.0
Ballibierna (BA)	42.630	0.560	1600	36.4 ± 1.4	88.1	0.0	0.0

The percentage of trees severely defoliated (defoliation > 50 %) and with mistletoe infestation degree ≥ 3 are also shown. Diameter values are means ± SE.

a semi-quantitative scale from 0 (no cone) to 3 (abundant cones) as the coning index of continental data.

To quantify radial growth patterns in each stand, 10–20 trees were cored at 1.3 m using a Pressler increment borer. Two cores were taken per tree and mean tree-ring widths (period 1984–2020) were calculated for each stand using dendrochronological methods (Fritts, 1976). Ring width was converted into basal area increment (BAI) and mean values of both variables were calculated for the period 1990–2000 at the tree level. Tree age at 1.3 m was estimated by counting the number of rings in the core with more rings presenting pith or innermost curved rings. We did not estimate tree age considering the years that trees take to reach 1.3 m to avoid adding more uncertainty to age estimation. We also counted the number of historical releases suffered by each sampled tree. Historical growth releases, which we assumed to result mostly from past logging, were defined as periods with at least five consecutive years showing positive growth changes greater than 75 % during the period 1950–2000 (Camarero et al., 2011). Other causes of releases such as local-scale blowdowns were discarded by avoiding uprooted trees or trees with stem breakage.

The transect data were taken in 2020–2023 and they were compared and combined with more detailed plot-based data obtained from 20 silver fir stands sampled in 1999–2000 (Camarero et al., 2011; Gazol and Camarero, 2016). In short, the following variables were obtained at tree level (n = 360 trees): longitude, latitude, elevation, northness, soil type (0, basic soil; 1, acid soil), ratio between summer precipitation (period 1990–2000) and slope steepness (a surrogate of water availability during the growing season), tree age and dbh, tree defoliation, mean ring-width, competition index, density and basal area of beech and frequency of releases.

A circular plot with a radius of 7.6 m was located around each focal

tree and all trees taller than 1.3 m were identified, and their diameter was recorded. This allowed us to obtain basal area and stem density values for each tree. Then, a competition index was calculated based on the diameters of the focal silver fir and its neighbors (Lorimer, 1983). We paid special attention to the density of species which produce fruits in winter because they can feed some bird species (e.g., *Turdus viscivorus*) which disperse mistletoe berries (Zuber, 2004). Specifically, we focused on *Sorbus aria*, a fleshy-fruit service tree whose berries ripen in autumn, are eaten and dispersed by birds and may stay on the twigs during winter (Aldasoro et al., 2004). Precipitation data were obtained from a Spanish 0.1°-gridded monthly dataset (Beguería et al., 2023).

2.3. Data on mistletoe infestation level, cone production and regeneration at local scale

At local scale, we selected two of the stands with highest mistletoe infestation levels (Paco de Villanúa –hereafter site VI, Selva Negra –hereafter site SN). There, in addition to tree growth data, obtained in 2000, cone production and silver fir regeneration were also evaluated. Cone production was estimated by counting the number of rachises and cones along the crown of sampled trees during 1 minute and using binoculars. This was done in 33 trees per site and during early to mid-October 2023, when most cones have disappeared, their seeds have been already dispersed but the rachises persist and are visible in the upper crown. In addition, tree diameter and height, total crown defoliation and defoliation of the uppermost third crown section were measured. Lastly, silver fir seed production was estimated by counting the number of seeds in four 25-cm² quadrats randomly located within a circular plot of radius 7.6 m centered in each sampled tree.

In these two sites, mean series of BAI were calculated for lightly

(infestation degree < 3) and heavily (infestation degree ≥ 3) infested trees to compare them. In addition, to assess changes in growth trends BAI slopes (linear trends) were also calculated for the two classes of trees considering 20-year running intervals.

2.4. Attribution analyses of vigor, growth and cone production at regional scale

To examine relationships between variables we calculated Spearman correlations (r_s). We also compared characteristics (diameter, height, defoliation and infestation levels, number of cones and seed density) between sites and between infestation classes within sites using Mann-Whitney tests. To compare BAI series between lightly or heavily infested trees, non-parametric Wilcoxon rank-sum W tests were used. In the two intensively studied sites, zero-inflated Poisson models were fitted to the cone production of silver fir as a function of crown defoliation or mistletoe infestation. To improve the model fitness, we used data of defoliation of the uppermost third crown section. The zero-inflated Poisson models were fitted using the *pscl* R package (Jackman, 2024).

First, at continental scale, generalized linear mixed-effects models (GLMMs, Bates et al., 2015) were used to study the relationships between defoliation and the extent of mistletoe infestation in the period 2004–2019. Defoliation was log-transformed prior to the analyses and we fitted Gaussian models using the country crossed with the tree nested within the plot as random effects. We also used GLMMs to study the effect of mistletoe presence, extent of damage and defoliation on cone production. We fitted binomial models using the country crossed with the tree nested within the plot as random effects. In the two situations, the most parsimonious models were selected based on the Akaike Information Criterion (AIC). The GLMM analyses were done with the package *lme4* (Bates et al., 2015) and the models were selected with the package *MuMIn* (Barton, 2024) in the R statistical software (R Development Core Team, 2025).

Second, we used Structural Equation Models (SEMs) to evaluate the importance of environmental, structural, and historical variables as drivers of silver fir crown defoliation, tree growth (BAI) and mistletoe

infestation degree at the regional scale ($n = 30$ sites, $n = 360$ trees). This multivariate framework allows testing whether the variance-covariance matrix obtained from observational data differs from the matrix derived from hypothetical models (Grace, 2006). SEMs deal with the interdependence of variables and allow: (i) decomposing total effects in direct and indirect types and (ii) comparing alternative models using indices of goodness of fit (Mitchell, 1992). To estimate the standardized path coefficients, which quantify the strength of the associations among variables, we used a robust Maximum Likelihood method because all variables excepting BAI deviated from normality even after log-transformation (Bentler and Wu, 2002). The use of several indices to evaluate the model fitness provides a robust assessment of fitted SEMs (Jöreskog, 1993). Hence, we evaluated the models using: the χ^2 test and its probability level (p), as well as several complementary goodness-of-fit indices (AGFI, Adjusted Goodness-of-Fit Index; RMSEA, Root Mean Square Error of Approximation; AIC). Values close to zero of the RMSEA statistic and values close to one of AGFI would indicate that the evaluated model is consistent with the theoretical model (see Fig. S2). In relative terms, models with high p values associated with χ^2 correspond to better fitted models. The proportion of observed variance of dependent variables (R^2) was also calculated. The most parsimonious fitted model was selected by minimizing the AIC. SEMs were fitted using the program EQS ver. 6.4 (Bentler and Wu, 2002; Bentler, 2006). Tree-level explanatory variables were: geographical coordinates and elevation (obtained with a GPS at ± 5 m resolution), northness, soil type, the ratio between summer rainfall and slope, tree age and diameter, competition index, density and basal area of European beech and frequency of releases. Cone production was not considered in the SEM, but in the random forest models which are more versatile (Breiman, 2001).

Third, we fitted three random forest models with growth, defoliation and cone production as response variables, respectively, using the regional silver fir data. All other measurements were included as predictors. Breiman (2001) random forest algorithm was applied using the *randomForest* (Liaw and Wiener, 2002) package of the R statistical software (R Development Core Team, 2025). We built 1000 decision

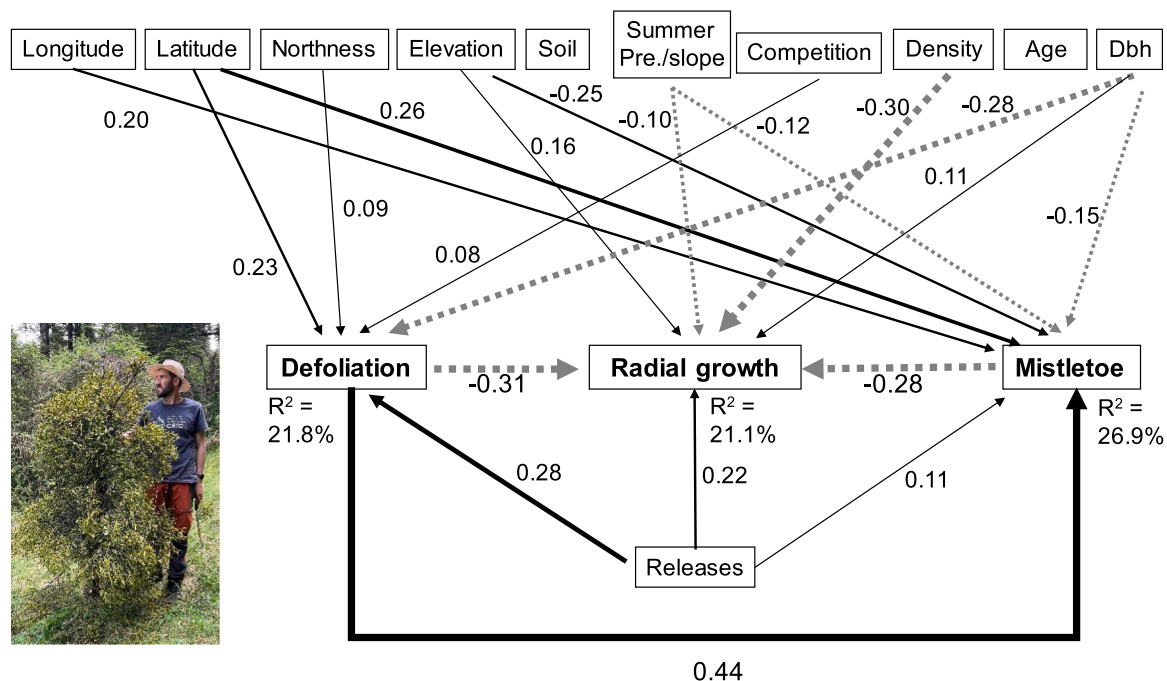


Fig. 3. SEM diagram showing the main drivers of vigor and growth in Pyrenean silver fir forests. Only significant ($p < 0.05$) relationships are shown. Black continuous arrows show positive effects, whereas grey dotted arrows show negative effects. The percentage of explained variance (R^2) is shown in the case of crown defoliation, radial growth and mistletoe abundance. The thicker the arrow, the stronger the effect (in absolute terms). The image shows one of the authors (AG) holding a silver fir apex completely infested by mistletoe.

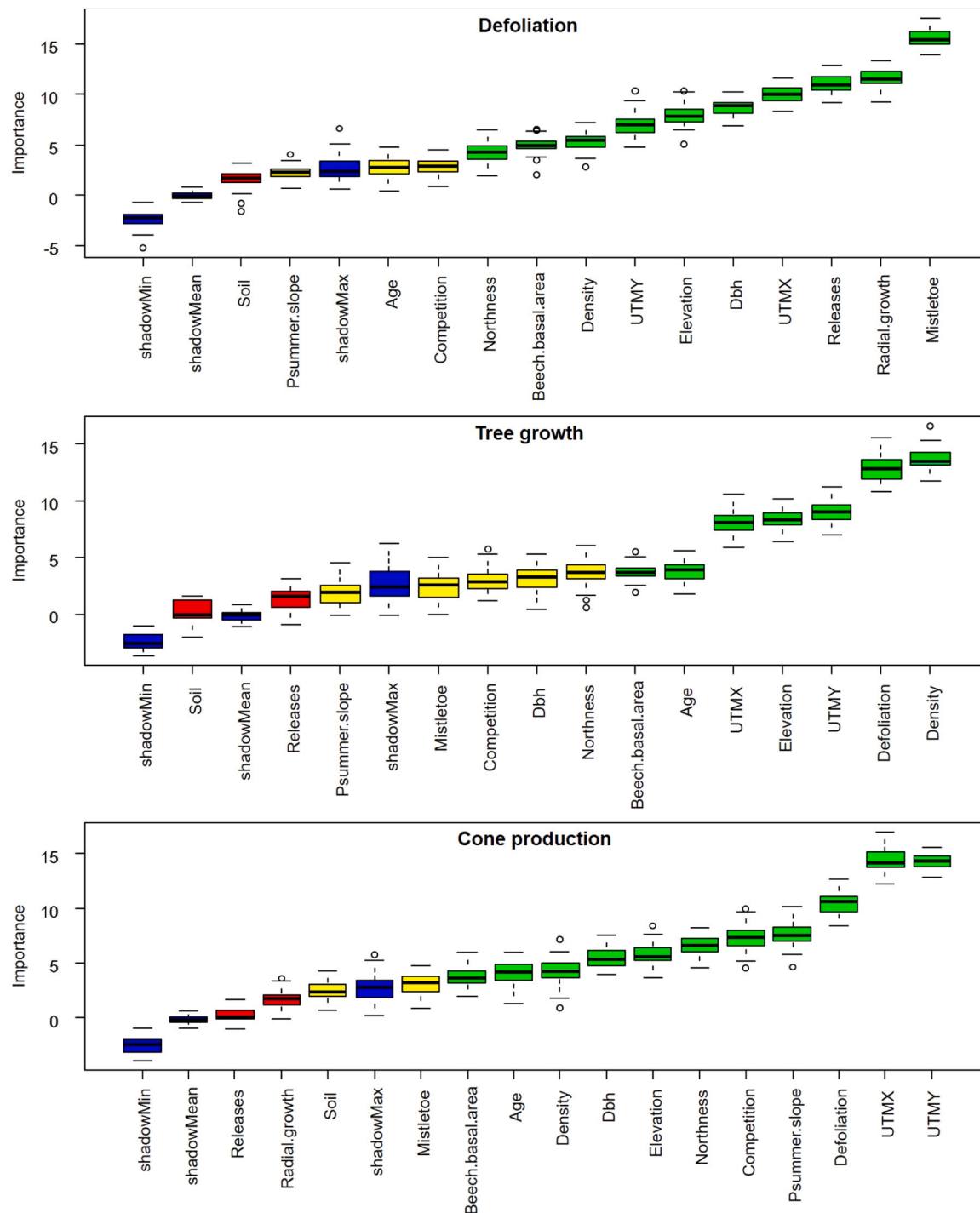


Fig. 4. Variable importance (Z-scores) according to the random forest models fitted for the response variables (crown defoliation, tree growth and cone production) in the study silver fir stands. Blue box-plots correspond to minimal, average and maximum Z-scores of a random predictor. Green, yellow and red box-plots represent Z-scores of important, marginal and discardable predictors, respectively. Dbh is the diameter measured at breast height, growth is the mean ring-width, P summer slope is the ratio between summer precipitation and slope, and UTMX and UTMY indicate longitude and latitude, respectively.

trees to fit each model to the training data. The goodness of fit of the models was assessed by calculating the values predicted by the three models from the test data and obtaining the R^2 of the linear models relating the predicted values to the actual values. The training data were obtained by randomly selecting 80 % of the sampled silver fir individuals. The remaining 20 % were the test data. We assessed the importance of the predictor variables by calculating Z-scores using the Boruta package in R (Kursa and Rudnicki, 2010). To obtain Z-scores, we first calculated the loss of classification accuracy caused by the random

permutation of variable values between silver fir individuals. This was done separately for all trees of each random forest model which use a given attribute for classification. The Z-score was calculated by dividing the average loss by its standard deviation (Kursa and Rudnicki, 2010). The Z-score of the predictors was compared with that of random variables and the predictors were classified as important, marginal and discardable (confirmed, tentative and rejected, respectively, according to Kursa and Rudnicki, 2010) depending on whether the predictors have significantly higher Z-scores than the random variables (important

predictors), the Z-score of the predictors does not differ from that of the random variables (discardable predictors), or when the maximum number of iterations (set at 100) is reached without being able to determine whether the Z-scores significantly differ (marginal predictors).

3. Results

3.1. Mistletoe impacts on European silver fir forests

According to ICP-forests data, mistletoe was abundant in silver fir forests from central Europe at least since 2019 (Fig. 1 and S1). Mistletoe was also detected in marginal populations of the silver fir distribution area located in southern Italy or the western Pyrenees. The percentage of infested silver firs has been steadily increasing, but defoliation peaked in 2012 and 2019 with values of ca. 24 % (Fig. 1b). At continental scale, we found no relationship between defoliation, mistletoe abundance and cone production.

3.2. Mistletoe impacts on Pyrenean silver fir forests

We found 12 sites where defoliation increased from the 2000s to the 2020 s, 4 sites where defoliation levels were similar and 14 sites where defoliation decreased (Table 1 and Fig. 2a). Dieback hotspots corresponded to low-elevation sites located in the westernmost area of the study region. Some of the most affected sites presented high mistletoe infestation levels (e.g., Lopetón – LO, Puente de Corralones –PC, Paco de Villanúa-low –VI), but this was not always the case (e.g., sites Paco Ezpela-low –PZ; Fig. 2b).

At tree level, mistletoe infestation was severe (≥ 3) in 70 out of the 360 measured trees, i.e. 19 %, whereas defoliation was severe (≥ 50 %) in 10 % of the sampled trees. We found positive relationships between mistletoe infestation level and crown defoliation at the site ($r_s = 0.37$; $p = 0.044$, $n = 30$) and tree levels ($r_s = 0.54$; $p < 0.001$, $n = 360$). That is, heavily infested sites and trees tended to show high defoliation (Fig. S3).

The selected SEM showed a robust fit ($\chi^2 = 23.61$, $p = 0.21$; AGFI = 0.96, RMSEA = 0.02; Fig. 3). It explained 21.8 % and 26.9 % of the crown defoliation and mistletoe infestation variability, respectively. Mistletoe infestation increased northwards and at lower elevation, and it was positively related to defoliation. Growth decreased as stem density, defoliation and mistletoe infestation increased. Heavily infested trees showed lower growth rates than non-infested trees (Fig. S4). Crown defoliation increased northwards and in stands with stems of smaller diameter and showing more releases.

The random forests models explained 54 %, 27 % and 28 % of defoliation, growth and cone production variability, respectively. Defoliation was positively related to the mistletoe infestation degree (Figs. 3 and 4; Fig. S5). Other important predictors selected in the defoliation model were: growth (inverse relationship), number of releases (direct relationship), longitude (inverse relationship, i.e. higher defoliation westwards), tree diameter (inverse relationship for the dbh range between 30 and 50 cm), elevation (inverse relationship with high defoliation below 1400 m), latitude (inverse relationship), stem density (inverse relationship for low to intermediate values), beech basal area (direct relationship; range 1–41 m² ha⁻¹) and slope aspect (direct relationship).

In the growth model, the two most important predictors were density and defoliation, both showing inverse relationships, followed by topographical variables (latitude, longitude, elevation). Growth decreased below 1300 m (Fig. 4 and Fig. S6), and it was also directly related with tree age and beech basal area.

In the model of cone production, the most important predictors were latitude (direct relationship) and longitude (inverse relationship) followed by defoliation (inverse relationship; Fig. 4 and Fig. S7). Dry summers and more southern exposures were also related to high cone

Table 2

Statistics of zero-inflated Poisson models fitted to the cone production of silver fir as a function of upper crown defoliation or mistletoe infestation. Models were fitted to data from the two study sites, Paco de Villanúa (VI) and Selva Negra (SN).

Site (code)	Predictor	Estimate	SE	z value	p value
Paco de Villanúa (VI)	Intercept	1.6344	0.1765	9.262	< 0.001
	Defoliation	−0.023	0.0097	−2.376	0.017
	Intercept	2.0190	0.2232	9.046	< 0.001
	Mistletoe	−0.4926	0.1471	−3.349	0.001
Selva Negra (SN)	Intercept	2.1962	0.09573	22.941	< 0.001
	Defoliation	−0.036	0.0168	−2.153	0.031
	Intercept	2.10482	0.1138	18.501	< 0.001
	Mistletoe	−0.3601	0.1068	−2.957	0.002

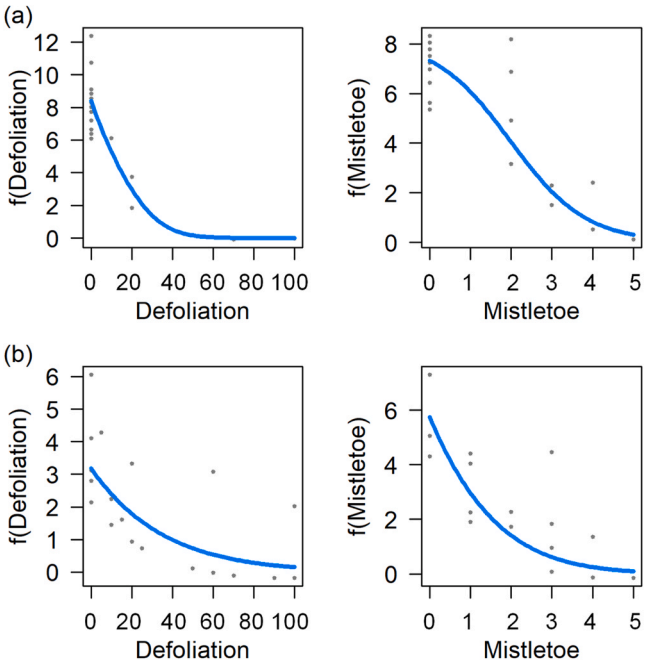


Fig. 5. Predicted cone production in silver fir trees as a function of upper crown defoliation (%) or mistletoe infestation (0–6) in the two study sites (a, Paco de Villanúa; b, Selva Negra). Fitted curves correspond to zero-inflated Poisson models (see Table 2).

production, which also increased in sites with more competition. Cone production also increased for trees with thick stems and those under 100 years of age, but decreased in stands with higher density and greater beech basal area.

3.3. Mistletoe impacts on the local silver fir forests

In sites VI and SN, the infestation degrees were (mean $\pm$ SE) 2.6 $\pm$ 0.2 and 2.3 $\pm$ 0.3, respectively (Table S1). Sampled trees showed similar height (ca. 17 m) and crown defoliation (51 %) in both sites, albeit diameter was larger in VI than in SN. Among sampled trees, 36 % and 44 % of them had cones or rachises in sites VI and SN, respectively. The mistletoe infestation degree and crown defoliation were positively correlated in both sites (VI, $r_s = 0.74$; SN, $r_s = 0.60$; $p < 0.001$ in both cases). The number of rachises and cones were negatively correlated with the defoliation level (VI, $r_s = -0.52$; SN, $r_s = -0.85$; $p < 0.01$ in both cases) and with the mistletoe infestation degree (VI, $r_s = -0.49$; SN, $r_s = -0.64$; $p < 0.01$ in both cases). Silver fir seed density was also negatively related to the mistletoe infestation degree (VI, $r_s = -0.38$; SN, $r_s = -0.39$; $p = 0.02$ in both cases). These negative associations with mistletoe infestation degree estimated for the whole tree crown were

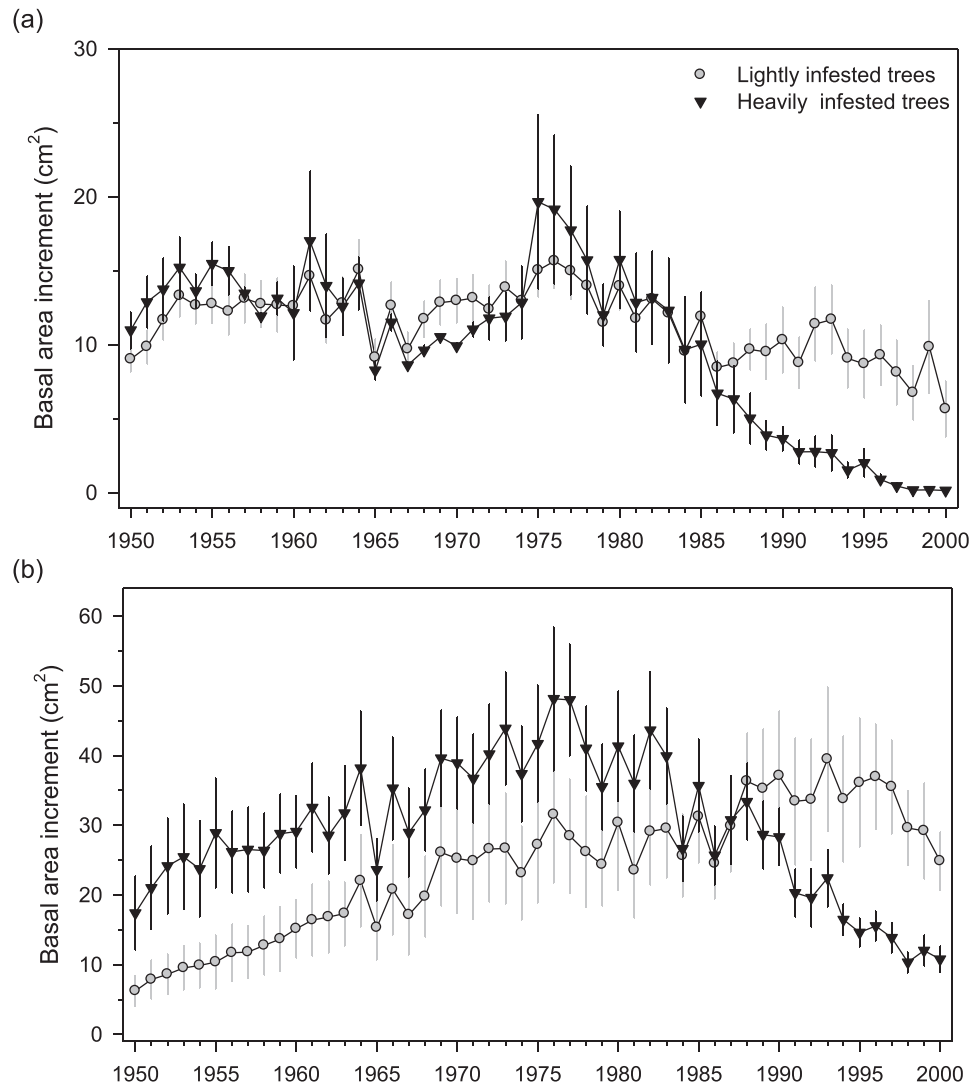


Fig. 6. Changes in basal area increment (BAI) in the (a) Paco de Villanúa (VI site) and (b) Selva Negra (SN) study sites considering silver fir trees with heavy and light mistletoe infestation degrees. Values are means $\pm$ SE.

also significant when considering infestation degrees for the middle or uppermost crown sectors. The zero-inflated Poisson models showed that cone production was inversely related to defoliation and mistletoe infestation (Table 2, Fig. 5).

Regarding growth data, heavily infested trees showed lower BAI than lightly infested trees 13 and 11 years before sampling in sites VI and SN, respectively (site VI, $W = 91$, $p = 0.0002$; site SN, $W = 78$, $p = 0.0005$; Fig. 6). On average, BAI of heavily infested trees was 22 % (site VI) and 53 % (site SN) of that of lightly infested trees during these 11- to 13-year-long divergence periods.

Heavily infested trees showed lower BAI slopes than lightly infested trees 12 and 15 years before sampling in sites VI ($W = 91$, $p = 0.0002$) and SN ($W = 66$, $p < 0.01$), respectively (Fig. 7).

4. Discussion

We found that silver fir crown defoliation was linked to severe mistletoe infestation and reduced radial growth. Specifically, the loss of needles in the uppermost third crown explains the decrease in cone production observed at local scale, thus constraining silver fir regeneration. Mistletoe uptakes nutrients from hosts and can contribute to hydraulic impairment by increasing the water loss through their leaves

leading to canopy dieback (Zweifel et al., 2012; Yan et al., 2016). Defoliated upper crowns and apices are associated to a lower cone production (Dobrowolska et al., 2017), albeit we did not measure the number of seeds produced per cone or their viability. Nevertheless, severely infested stands showed also a lower silver fir seed density. This may be explained by a lower cone production or by the opening of gaps leading to adverse microclimate conditions for seed germination (e.g., sunny conditions, higher vapor pressure deficit) and higher seed predation. More open and warmer microclimates are adverse for silver fir seedling establishment and growth in the understory given the shade-tolerance of this species (Aussenac, 2000). Regarding cone production, we assumed that during 2023 the silver fir crop was moderately high. In another Pyrenean silver fir stand (Gamüeta, see Table 1) where seed production has been annually measured since 2001 (González de Andrés et al., 2014), the seed production in 2023 (153 seeds m^{-2}) was significantly higher ($t = 3.94$, $p = 0.0007$) than the long-term mean (mean $\pm$ SE, 85 ± 17 seeds m^{-2}).

The European-wide assessment of silver fir forests provided by ICP-forests data failed to find a strong relationship between mistletoe infestation and crown defoliation. This may be an aspect to improve in this continental network because estimates of mistletoe incidence may be too coarse or geographically biased towards some regions (e.g.,

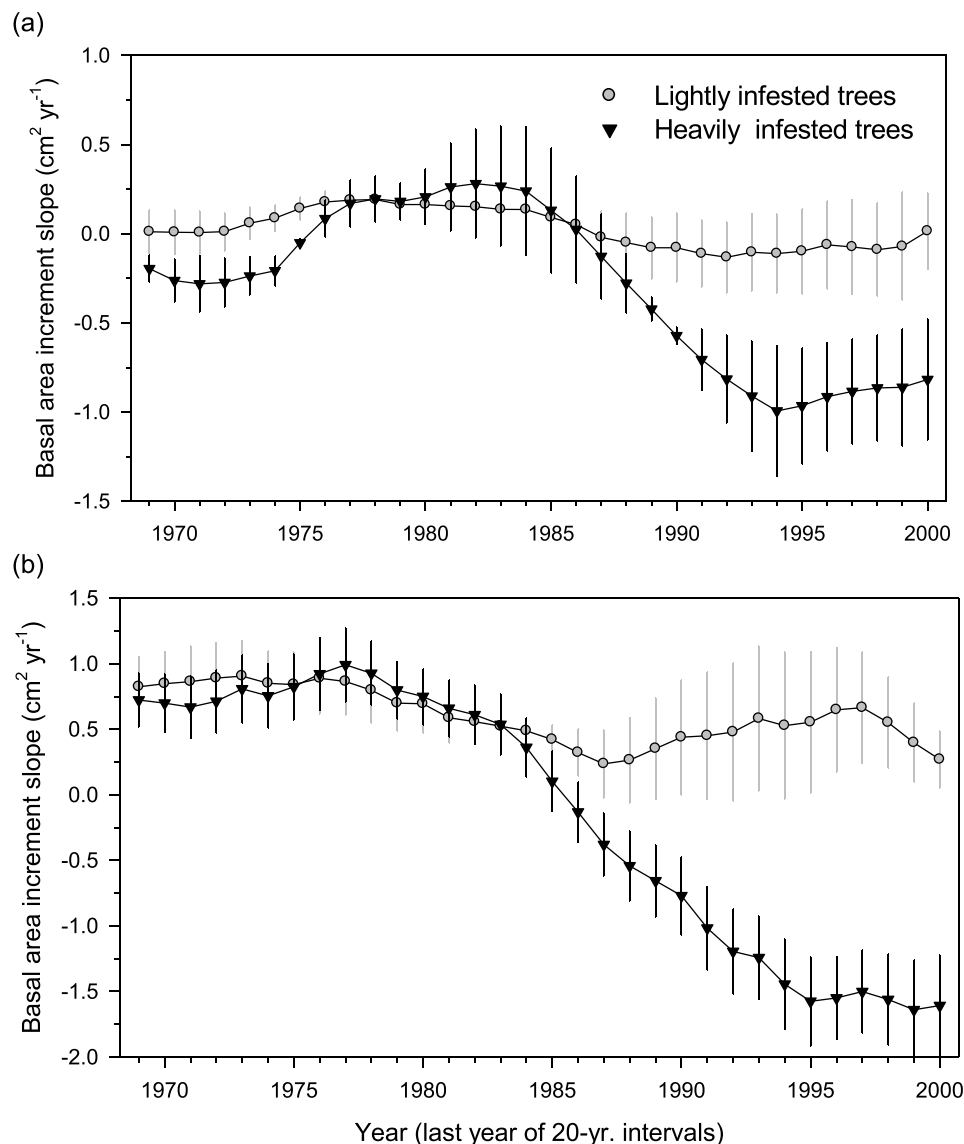


Fig. 7. Changes in BAI slope in the (a) Paco de Villanúa (VI site) and (b) Selva Negra (SN) study sites calculated for 20-year intervals for slightly and heavily infested trees, respectively. Values are means $\pm$ SE.

central Europe). Our findings suggest that these broad-scale assessments would gain predictive power by refining local estimates of mistletoe abundance. Nonetheless, the patterns detected by ICP-forests data agree with our regional and local analyses, namely, an increase of mistletoe infestation and localized and punctual increases of mistletoe-induced crown defoliation.

At regional scale, crown defoliation increased as mistletoe infestation did, but infestation only affected 19 % of the measured trees, whereas dieback affected more stands and showed a different geographic pattern. This suggests that mistletoe contributed to silver fir dieback in some of the study Pyrenean forests, but it was not the main driver. The most plausible key drivers of silver fir dieback in this region are warmer late-summer conditions leading to high evaporative water demand (Gazol et al., 2020; Crespo-Antia et al., 2024) and fungal pathogens such as *Heterobasidion abietinum* (Oliva and Colinas, 2007, 2010). Future studies could investigate whether the three stressors interact and trigger silver fir dieback. Historical factors should be also considered, as indicated the influence of historical releases, because stands formerly logged could be dominated by slow-growing trees, which may be predisposed to drought-induced dieback (Camarero et al., 2011). Overall, low-elevation stands were more prone to show lower

growth rates and higher mistletoe infestation levels.

Our models (SEM, random forests) offer synthetic views of the main variables affecting mistletoe infestation and silver fir defoliation. However, they are just statistical descriptions and contain uncertainties. For instance, the basal area of European beech showed direct relationships with defoliation, growth and cone production. This may be due to the dominance of mixed forests or to interactions with other variables not accounted for by random forest models, but which are reflected by direct and indirect effects in the SEM. That is an advantage of SEMs, but a drawback is that they assume linear relationships among variables and require large sample sizes (Grace, 2006).

At local scale, the different growth responses to mistletoe infestation may be due to the different long-term productivity and growth rates found in the two study sites, with higher mean BAI values in site SN ($26.7 \text{ cm}^2 \text{yr}^{-1}$) than in site VI ($10.7 \text{ cm}^2 \text{yr}^{-1}$). The period of growth divergence between lightly and heavily infested trees lasted 11–15 years according to BAI or BAI-slope data, which is shorter than that observed in infested Scots pine forests (21–34 years; Camarero et al., 2019), but similar to that found in silver firs from a nearby stand (González de Andrés et al., 2024a). The divergence period can be related to the mistletoe population exponential growth which lasts 10–12

years (Noetzli et al., 2003), and triggers growth decline and a loss of post-drought growth resilience (González de Andrés et al., 2024a).

The fitted statistical models could not account for less representative variables not measured in all sampled sites, but which are relevant for understanding mistletoe expansion. For instance, in silver fir stands with more trees heavily infested by mistletoe the density of *S. aria* increased (Fig. S8). This is expectable because this is one of the main fleshy-fruited species in mixed silver-fir stands which feeds birds during winter enhancing the dispersal and consumption of mistletoe berries. As an alternative management measure, mistletoe infestation could be directed or confined towards mixed stands where there are abundant individuals of winter fleshy-fruited species (e.g., whitebeams, rowans, holly, blackthorn, hawthorn, dog rose, etc.)

5. Conclusions

At continental and regional scales, the percentage of silver fir infested by mistletoe ranged 15–19 % of individuals. In the Spanish Pyrenees, stands showing severe defoliation and mistletoe infestation were spatially clustered and disjunct. Trees with defoliated upper crowns and severely infested by mistletoe tended to produce less cones and grew less as compared with lightly or non-infested trees. These differences were found at the regional and local scales. A lower cone production was also related to a lower seed density. In severely infested stands, the exponential phase of growth of mistletoe populations is rapid and may lead to severe growth decline and tree death in ca. 15–20 years. Under the observed warmer conditions affecting rear-edge Pyrenean silver fir forests, infested stands should be carefully managed to prevent further mistletoe spread. This could be achieved by creating more structurally and compositionally diverse stands or by reducing the presence of winter fleshy-fruited tree and shrub species which attract birds acting as mistletoe vectors.

CRedit authorship contribution statement

Gazol Antonio: Writing – review & editing, Supervision, Software, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Gonzalez de Andres Ester:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation. **Rubio-Cuadrado Alvaro:** Writing – review & editing, Visualization, Software, Resources, Methodology, Investigation, Formal analysis. **Camarero J. Julio:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank J.A. Sesé for his during field sampling in Villanúa. This study was funded by projects PID2021–123675OB-C43 and TED2021–129770B-C21 (Spanish Ministry of Science and Innovation), and by Gobierno de Aragón (contract for silver fir monitoring) and CSIC (grant PIE-20223AT003). ARC acknowledges support by “Margarita Salas” postdoctoral fellowship (reference RCMS-22-G1T6IW-17-NLHJ80) of the Universidad Politécnica de Madrid. We thank the data access and support provided by the Programme Coordinating Centre and the Expert Panels of ICP Forests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122693.

Data availability

Data will be made available on request.

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