



Development and long-term dynamics of old-growth beech-fir forests in the Pyrenees: Evidence from dendroecology and dynamic vegetation modelling

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ABSTRACT

Ecological knowledge on long-term forest dynamics and development has been primarily derived from the study of old-growth forests. Centuries of forest management have decreased the extent of temperate old-growth forests in Europe and altered managed forests. Disentangling the effects of past human disturbances and climate on current species composition is crucial for understanding the long-term development of forests under global change. In this study, we investigated disturbance and recruitment dynamics in two forests in the Western Pyrenees (Spain) with contrasting management history: an old-growth forest and a long-untouched forest, both dominated by the two shade-tolerant species *Fagus sylvatica* (European beech) and *Abies alba* (Silver fir). We used dendroecological methods in seven plots to analyse forest structure, growth patterns and disturbance histories in these forests. We benchmarked these data with the dynamic vegetation model ForClim to examine the effects of natural and human-induced disturbances on forest development, structure and species composition. Disturbance regimes differed between the study forests, but none showed evidence of stand replacing disturbances, either natural or human induced. Low disturbance rates and continuous recruitment of beech and fir dominated the old-growth forest over the last 400 years. In contrast, the long-untouched forest was intensively disturbed in 1700–1780, probably by logging, with lower natural disturbance rates thereafter. Beech and fir recruitment preferentially occurred after more intense disturbances, despite the high shade tolerance of both beech and fir. Higher fir abundance in the long-untouched forest than in the old-growth forest appeared to be related to its human-induced disturbances. ForClim closely simulated forest potential natural vegetation with a dominance of beech over fir, but overestimated the presence of less shade-tolerant species. Previously observed local fir decline may result from natural forest successional processes after logging. Within ~200 years after logging cessation, some long-untouched forest structural attributes converged towards old-growth forest, but legacy effects still affected species composition and structure. Natural disturbance regimes in beech-fir forests of the Western Pyrenees induce temporal fluctuations between beech and fir abundance, with a natural tendency for beech dominance in advanced developmental stages with low disturbance rates.

1. Introduction

Disturbances are a major factor driving the developmental process of forests, affecting their productivity, composition, and structure at different spatial and temporal scales (Bormann and Likens, 1979; Nagel et al., 2021). Natural and human induced disturbances have different effects on ecosystem behaviour that may last for decades or centuries. Much of our understanding on natural disturbance regimes in temperate

forests and their effects originates from the study of old-growth forests (Piovesan et al., 2005; Fraver et al., 2009; Nagel et al., 2014; Martin-Benito et al., 2020). These forests are governed by intermediate disturbance regimes (Woods, 2004), i.e. natural disturbance regimes dominated by frequent endogenous disturbances caused by the death of single trees (gap dynamics) superimposed onto larger exogenous disturbances. In the absence of catastrophic, stand replacing disturbances, these asynchronous dynamics maintain stands at different stages of

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development, promoting structural (age, sizes) and functional (species, deadwood volume) heterogeneity (Glitzenstein et al., 1986; Nagel et al., 2021). These forests may not necessarily be in a steady state as they may still undergo compositional changes influenced by different disturbance frequency and intensity. In contrast, management practices commonly result in more homogenous, even-aged stands with regular structure and lower species diversity (McGee et al., 1999). Biomass accumulation in managed forests tends to show more regular cyclic patterns than in unmanaged forests. Ecosystem changes induced by natural and human disturbances condition forest development for centuries. Understanding the long-term legacies of different disturbance regimes is essential to anticipate future forest changes in a period of globally increasing disturbances (Seidl et al., 2017).

In Europe, centuries of intensive forest management have made old-growth forests extremely rare (Sabatini et al., 2018). Most studies of natural dynamics in temperate forests in Europe are based on old-growth forest remnants from eastern Europe (Splechtna et al., 2005; Nagel et al., 2010; Sitzia et al., 2012; Trotsiuk et al., 2012; Nagel et al., 2014). Just a few studies have focused on old-growth forests from southern Europe (Piovesan et al., 2005; Martin-Benito et al., 2021), where some temperate species are close to their southern distributional limits and drought may be a stronger limiting factor (Piovesan et al., 2008; Camarero et al., 2011). In the Pyrenees, previous dendroecological studies in beech-fir forests have focused on the effects of human induced disturbances on fir decline (Camarero et al., 2011) or biomass accumulation (Molina-Valero et al., 2021). In contrast, natural forest disturbance regimes in the absence of or under very limited human intervention have not been explored. Some forests considered to be old-growth may actually be long-untouched forests (Buchwald, 2005; Wirth et al., 2009) i.e. they were logged to some degree but left unmanaged for centuries. In contrast, old-growth forests have no signs of any human interference with natural dynamics (Korpel, 1995; Buchwald, 2005). Long-untouched forests may be more abundant than old-growth forests, particularly in Europe (Sabatini et al., 2018). Ecological dynamics derived from these long-untouched forests may be more representative and applicable to a wider range of forests in different states of conservation or management than old-growth forests. Forestry management aimed at maintaining and restoring the structural heterogeneity and biodiversity is commonly derived from the study of frequency and intensity of natural disturbances that have shaped old-growth forests. Long-term effects of forest management may be derived from the comparative analysis between old-growth and long-untouched forests in terms of species composition, structure, biomass or carbon fixation (Albrich et al., 2021).

Few studies have examined the role of disturbances, either natural or human-induced, on forest dynamics, species composition and ecological processes in forests of western European Mountains. The coexistence of European beech and silver fir in these forests may be affected by ecological traits such as tolerance to drought and shade. While shade tolerance is high in both species (Leuschner and Meier, 2018), beech may be slightly more drought tolerant (Niinemets and Valladares, 2006). For example, most studies in the Pyrenees analyzed the effects of climate on tree growth and forest decline and show that beech and fir are mostly limited by drought at their southern distribution limits (Gazol et al., 2019). Silver fir decline in the Pyrenees over the last few decades has been attributed to increased warming and drought intensification combined with human induced disturbances (Camarero et al., 2011; Linares and Camarero, 2012). The species, however, regenerates and thrives under humid Mediterranean conditions (Walder et al., 2021) and may continue to do so in the future (Vitasse et al., 2019). Human interventions, however, may have reduced its presence and abundance because it was preferentially logged in beech-fir forests (Villar Pérez, 1980). Logging may predispose remaining fir trees to increased mortality (Gil Pelegrín et al., 2008; Camarero et al., 2011) but silver fir regenerates abundantly in logging created gaps (Cabrera, 2001). Species ecology in old-growth forests can serve as a reference of how species

coexist in the absence of major human influences and disentangle the effects of past human disturbances and climate on species composition or differential decline. Increased knowledge on forest disturbances also contributes to the development of closer-to-nature forest management approaches for surrounding or similar forests. Silvicultural systems that mimic natural processes in a closer-to-nature silviculture are essential towards active management that aims to restore the high structural complexity and biodiversity of old-growth temperate forests (Bauhus et al., 2009).

The main objective of this study was to analyze the frequency, intensity and timing of forest disturbances and how they have affected forest development and dynamics in terms of structure and growth over the last several centuries in beech-fir forests in the Western Pyrenees. Here, we reconstruct the history of disturbance and recruitment of two well preserved, old forests with contrasting management histories: an old-growth stand and a stand affected by logging in a distant past. Specifically, our objectives were to: (1) describe the stand level structural attributes, (2) reconstruct the history of natural disturbances in beech-fir dominated forest landscapes from these two stands, (3) analyze the effect of disturbances on species coexistence and growth, and (4) compare current forest characteristics against potential natural vegetation simulated with ForClim, a dynamic vegetation model (DVM). First, we compared stand attributes and disturbance histories between both stands to verify the management history of both stands. We aimed to better understand how development of secondary forest converges towards old-growth characteristics, the time scales of this process, and its effects on forest composition and structure. Finally, we considered whether beech-fir mixed forests are ecologically stable in time or whether the mixture is variable in space and time with alternation in species dominance with time. We combined detailed forest inventories with dendroecological techniques and simulations from ForClim to describe forest structure and reconstruct the stand dynamics during the last four hundred years.

2. Material and methods

2.1. Study area

We conducted this study in two strict forest reserves containing remnants of old-growth forest or long-untouched forest dominated by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) in the Western Pyrenees, Northern Spain (Fig. 1). These forests fall within the Southwestern European mountainous beech forest (European Environment Agency, 2006), specifically within the Asperulo-Fagetum beech forests (UE habitat type code 9130) growing on calcareous bedrock (flysch, limestone, marl) (Olano and Peralta de Andrés, 2009). These sites were selected based on previous knowledge on their conservation conditions (Viers, 1955; Gil Pelegrín et al., 1989; Aragón-Ruano and Riezu Elizalde, 2021) and their old-growth characteristics for forests dominated by shade-tolerant and long-lived tree species like European beech and silver fir (Mosseler et al., 2003; Wirth et al., 2009): (1) uneven age and size structure and (2) no signs of any human interference with natural dynamics should be present such as cut logs, stumps, or trails. The Aztaparreta forest reserve (175 ha) comprises one of the few remaining old-growth temperate forests in Western Europe, without any known management in the past (Gil Pelegrín et al., 1989). At the Lizaroia forest reserve (65 ha), despite its old-growth characteristics, management presumably ceased in the late 18th century (Viers, 1955; Aragón-Ruano and Riezu Elizalde, 2021), probably in 1782 or 1783 (Aragón-Ruano, 2022). Lizaroia is currently considered a long-untouched forest (Horvat et al., 2018). These strict forest reserves have been protected since 1987 and no activities other than hiking and research are allowed. Previous dendrochronological research in these reserves (Molina-Valero et al., 2021) reported the presence of trees close to the maximum age of both species and showed that they represent the highest naturalness degree (Di Filippo et al., 2016) for mixed beech-fir

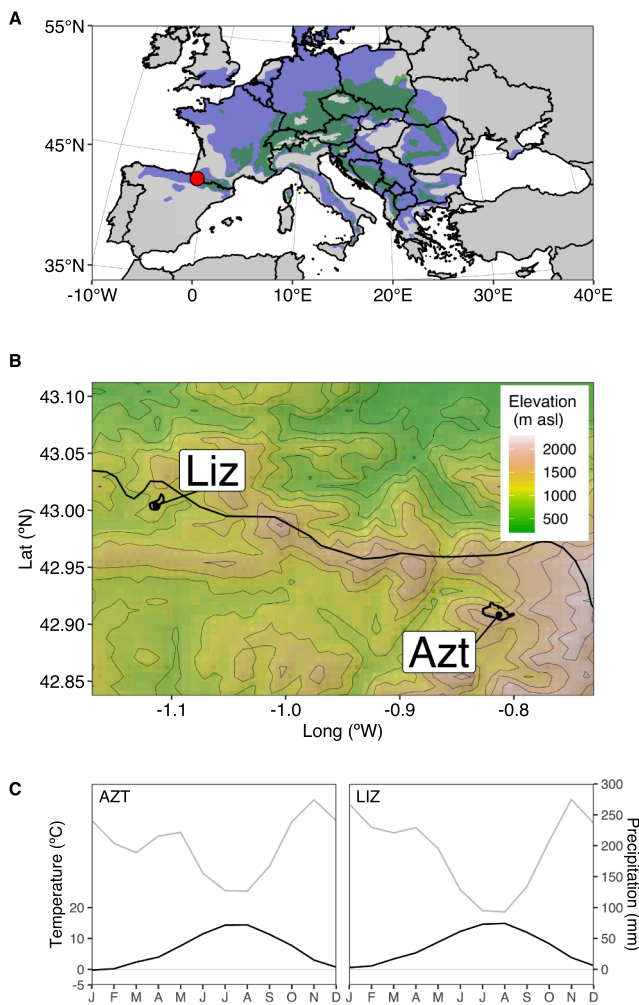


Fig. 1. Location of the two study sites. (A) Map of western Europe showing the location of the two study sites in northern Spain (red circle). Shaded areas show distribution ranges European beech (blue) and silver fir (green). (B) Detail map of the location of the two forest reserves: Lizardoia (LIZ) and Aztaparreta (AZT). (C) Climate diagrams in each of the reserves for the period 1970–2020 with mean monthly temperature (black; left y axis) and monthly precipitation sum (grey line; right y axis).

forest, with a slightly higher level of naturalness in Aztaparreta than in Lizardoia. Together, these reserves provide an ideal setting to investigate natural and human-induced disturbances and their effects on population dynamics, species composition, forest structure and forest development towards old-growth characteristics.

Both sites experience mountain, Atlantic (oceanic) climate with abundant precipitation evenly distributed throughout the year and no marked period of drought. We combined climate data for several nearby climate stations between 1970 and 2020 to estimate climate at our two study sites, also using monthly lapse rates. The two main stations were Irabia Dam (822 m a.s.l., 4.4 km from Lizardoia) and Ansó-Refugio de Linza (1350 m a.s.l., 2.1 km from Aztaparreta). The lower site Lizardoia (1080–1150 m a.s.l.) receives on average 2060 mm·year⁻¹ with a mean temperature of 7.62 °C while the higher site Aztaparreta (1500–1610 m a.s.l.) receives 2400 mm·year⁻¹ and has a mean temperature of 6.41 °C.

2.2. Field methods

We established a total of seven 60-m diameter plots (~2827 m² each) in fully stocked stands (i.e., containing as much tree biomass as resources allow at the site; Molina-Valero et al. 2021) with no sign of

recent disturbances, four in Aztaparreta and three in Lizardoia (Table 1). Each plot consisted of three concentric subplots with radius of 5 m, 20 m and 30 m. Within each subplot, the minimum selecting diameter at breast height (DBH) of trees was 5 cm, 15 cm and 30 cm, respectively (Martin-Benito et al., 2020; Martin-Benito et al., 2021). For all live or dead trees above the sampling threshold of each respective concentric subplot, we measured DBH, total height, and crown length (length from the lowest live branch to the top of the crown) and extracted increment cores at 1.30 m above the ground. For conservation reasons, only one core per tree was extracted. To extrapolate variables from tree to plot level data, we applied expansion factors to each tree depending on their concentric subplot (e.g. expansion factor for the 20-m subplot was 10,000 m² / [$\pi \cdot (20 \text{ m})^2$] \approx 7.958).

With this nested sampling design, we sought to balance the number of large, and potentially old, trees while simultaneously sampling smaller trees in a more efficient manner (Martin-Benito et al., 2020; Martin-Benito et al., 2021). This sampling allows to estimate forest growth chronologies at the stand level, which takes into account the growth and abundance of trees (Babst et al., 2014; Nehrbass-Ahles et al., 2014; Dye et al., 2016). In addition, including trees across a wide range of DBH reduces the false negative bias in disturbance detections at the end of the study period potentially arising from targeting old, dominant trees (McEwan et al., 2014). We sampled a total of 429 living and dead trees from the seven plots at the two forests.

In addition, we used a published survey of forest resources in Aztaparreta in 1988, whereby 47 plots with 20-m in radius (1256 m² each) located throughout the entire reserve were inventoried (Gil Pelegrín et al., 1989). Although the original raw data from that study was not available, published summaries allowed us to compare results with plots measured in 2018. We focused our comparisons on diameter distributions of beech because that was the most abundant species in 1988 (96.3 % of surveyed trees) and more data were available. A stand-wide estimation of fir basal area in 1988 allowed such comparison with the 2018 data. We limited our comparison to trees of DBH \geq 17.5 cm because that was the minimum sampling DBH in 1988.

2.3. Dendrochronological methods and disturbance analysis.

Increment cores were mounted, dried and then sanded until rings were clearly visible. Rings were visually crossdated and measured to a 0.01 mm precision on a LINTAB measuring station. Crossdating was verified with COFECHA (Holmes, 1983). For each tree, DBH and basal area increments (BAI) were reconstructed back in time by subtracting ring widths from measured DBH. DBH over bark was first converted to DBH under bark using bark thickness allometric equations for *Abies alba* (Stängle and Dormann, 2018) and *Fagus orientalis*, due to the lack of bark thickness equations for *Fagus sylvatica* (Bonyad et al., 2012). For cores that missed the pith, the number of rings to the pith was estimated based on curvature and growth of the innermost rings (Duncan, 1989). Estimating ages at coring height allows to infer dynamics in tree recruitment (i.e. trees reaching the minimum DBH threshold for sampling of 5 cm), as opposed to tree regeneration (i.e. years since seedling germination and establishment). Seedlings of shade-tolerant species may survive decades under shade with little growth and require decades to reach 5 cm DBH at coring height (i.e. recruit) (Nagel et al., 2014). Thus, our estimations of recruitment time underestimate time of tree establishment by 10 or more years (Klopčič and Boncina, 2012; Barna and Bosela, 2015).

We used tree-ring width time series to reconstruct events of past disturbance in these forests. Abrupt and sustained increases in tree growth in ring width series indicate sudden reductions in competition induced by disturbances (Lorimer, 1985). We used the radial growth averaging method (Lorimer and Frelich, 1989) because of its detection sensitivity and temporal accuracy (Trotsiuk et al., 2018). This method estimates the percentage growth changes (%GC) between two consecutive 10-year periods M1 and M2 as $GC = 100 \cdot [(M2 - M1) / (M1)]$, where

Table 1
Summary description of the trees inventoried and cored in the two forest reserves.

Site	Plots	Species ^a	Trees ^b	DBH (cm)		Height (m)		Age (years) ^d		Time span	\bar{r} ^e
				mean (SD) ^c	range	mean (SD)	range	mean (SD)	range		
Aztaparreta (AZT)	4	ABAL	27/19	83.4 (21.0)	52–123.4	33.5 (6.0)	16.9–41.0	200 (55.3)	109–287	1725–2017	0.549
		FASY	196/182	47.5 (17.6)	6.5–93.6	25.8 (5.0)	4.6–36.4	258 (103.0)	26–459	1559–2017	0.552
Lizardoia (LIZ)	3	ABAL	108/90	37.8 (19.0)	8.7–103.0	23.7 (8.1)	8.7–42.1	124 (53.3)	18–218	1800–2017	0.516
		FASY	138/134	51.7 (22.0)	7.0–105.4	31.8 (6.6)	9.4–42.7	202 (86.2)	42–378	1640–2017	0.507

^a, species codes are: ABAL (*Abies alba*) and FASY (*Fagus sylvatica*).

^b, inventoried/cores used. Some trees were inventoried but could not be cored.

^c, standard deviation.

^d, core time span.

^e, \bar{r} mean interseries correlation.

M1 and M2 are the mean radial growth before and after any considered year. We considered $50\% \leq GC < 100\%$ as minor growth releases and $GC \geq 100\%$ as major growth releases. Disturbance intensity was expressed as the percentage of trees recording a release. Disturbances were analyzed in R (R Core Team, 2019) using packages dplR (Bunn, 2008) and TRADER (Altman et al., 2014).

2.4. Aboveground biomass

We used two types of species-specific allometric equations to estimate woody above ground biomass (AGB) of each tree: i) equations requiring DBH and tree height (Ruiz-Peinado et al., 2011; Ruiz-Peinado et al., 2012) for AGB at the time of sampling (summer 2018) and ii) DBH-based equations (Montero et al., 2005) to estimate AGB retrospectively from tree-ring reconstructed DBH. For trees whose pith was not reached, we completed ring widths for missing years with the average annual ring width of trees within the same 5-cm DBH class. We estimated annual increments of AGB (AGBI) for every tree as the difference in AGB for two consecutive years. The sum of annual AGB increments of all individual trees was used as the AGBI per unit area (Graumlich et al., 1989; Dye et al., 2016). Previous studies show that AGB estimated from tree rings accurately represent stand AGB and AGBI for several decades (Dye et al., 2016; Klesse et al., 2016) particularly in the absence of large disturbances (Gea-Izquierdo and Sánchez-González, 2022). We estimated AGB in 1988, applying the same DBH-based allometric equations used for the 2018 sampling to a tree of average DBH within each 5-cm DBH classes and abundance of trees within those classes.

2.5. Forest development and potential natural vegetation

Information on old-growth forest structure and disturbance histories can be greatly complemented by results from dynamic vegetation models (DVMs) (Bormann and Likens, 1979; Bugmann, 2001). In turn, empirical data from old-growth forests can be used to benchmark DVMs (Thrippleton et al., 2021). These models can simulate forest development and structure in terms of stand density, tree size distributions, and species abundance based on environmental variables such as climate, soil properties, and topography. Simulation results after the system reaches steady state conditions can be assimilated to potential natural vegetation. Old-growth stand structure and species composition do not necessarily reflect potential natural vegetation because they are the result of many stochastic processes particularly disturbances with long-term legacy effects. However, comparing DVMs simulations under contrasting environmental conditions can offer great insight into the effects of disturbance on forest development, structure and species composition. Thus, we compared model simulations between our old-growth forest (Aztaparreta), potentially under rather steady-state dynamics, with those of an old, and well-preserved forest, but with previous human-induced disturbances centuries ago (Lizardoia). This

allowed to additionally gain insight into the time required for forests to recover and reach old-growth forest conditions after the cessation of human induced disturbances. We also compared forest productivity simulated by a DVM with productivity estimated using dendroecological methods. Simulated productivity was estimated from AGB increments of trees alive within the last 20 years of DVM simulations because our sampled plots also included dead trees.

We used the DVM ForClim v3.3.1, a forest succession model (gap model) thoroughly tested and validated for European temperate forests (Bugmann, 1996; Bugmann and Solomon, 2000). The model simulates species-specific basal area, stem numbers and diameter distributions for thirty European temperate tree species. ForClim simulates the establishment, growth, and mortality of trees on forest patches (area $\sim 830 \text{ m}^2$). Properties at stand level ($\sim 10 \text{ ha}$) can be estimated by averaging properties from 200 patches to reduce the effect of small-scale idiosyncrasies (Bormann and Likens, 1979; Bugmann, 2001). Tree establishment and growth are mainly regulated by growing degree-days, light availability, and soil moisture. In turn, degree-days are controlled by mean monthly temperature while soil moisture is controlled by monthly total precipitation, potential evapotranspiration and water holding capacity. Light availability is controlled by leaf area which emerges from model-internal feedbacks. How light availability affects trees depends on the species-specific light demands of seedlings and adult trees. Tree establishment is also controlled by browsing pressure, to which silver fir is particularly sensitive (Didion et al., 2011; Cailleret et al., 2014). Previous studies suggest that browsing pressure in the Pyrenees is low for silver fir, which is the most sensitive species to browsing in the area, and browsing is not a major limiting factor for fir regeneration (Ameztegui and Coll, 2015). Thus, we used low browsing pressure (ForClim parameter kBrPr = 5) in our simulations. Preliminary simulations with default species parameters for the maximum winter temperature tolerated by fir (ForClim parameter kWITX = -3°C ; Bugmann, 1996) showed that insufficient chilling due to high temperatures was almost entirely hindering fir regeneration in the area, contrary to field observations, suggesting that the default kWITX parameter value for silver fir in ForClim may be too low, in line with previous studies in Mediterranean climate (Vitasse et al., 2019). Thus, we increased the maximum winter temperature tolerated by fir to kWITX = -1°C (Table SM1) based on observation of abundant recruitment in the surroundings of our study forests (personal observation) and on climate data available on winter temperatures from our sites (Fig. 1). Uncertainty with maximum winter temperature tolerated by plants remains rather high because of insufficient understanding of species-specific processes and underlying mechanisms of dormancy release (Cooke et al., 2012).

Tree mortality in ForClim v3.3.1 is simulated as the combination of age-dependent background mortality and growth-dependent stress mortality. A constant age-dependent background mortality is based on species-specific maximum longevity, whereas stress mortality probability increases with successive years of very low relative and/or absolute radial growth (for further information on tree mortality in ForClim

see Bugmann, 1996; Bircher et al., 2015; Huber et al., 2020; Thrippleton et al., 2021). The model requires driving data in the form of long-term monthly mean temperature and precipitation sums as well as their standard deviations and cross-correlations. We used climate data between 1970 and 2020 to derive these variables. From these climate data, the model uses a weather generator to provide time series of monthly precipitation and temperature. For a complete model description see Bugmann and Solomon (2000). Out of the 30 tree species for which the ForClim model is parameterized, we limited the simulations to the 23 tree species that naturally occur in the temperate forests of the Pyrenees (Table SM1). The model was run for 2000 years from bare ground initial conditions to reach a steady state condition under current climatic conditions (i.e. 1970–2020). Transient dynamics for these forest stands were analysed from these 2000 years of simulations. At the end of their simulation period, average conditions of 200 patches can be considered to represent forest conditions in dynamic equilibrium at the ecosystem level.

3. Results

3.1. Forest structure and composition in beech-fir forests

The two forests differed in their relative species composition and structure (Fig. 2). Stem density in the old-growth forest Aztaparreta was lower than in the long-untouched forest Lizardoia (319 trees·ha⁻¹ vs 822 trees·ha⁻¹) and less variable between plots (216–414 trees·ha⁻¹ vs 294–1773 trees·ha⁻¹). Diameter distribution in Aztaparreta was characterized by a high number of small beech trees (93 trees·ha⁻¹; DBH < 10 cm), 11–20 beech trees·ha⁻¹ for sizes between 15 cm and 70 cm and a few larger beech trees up to 93.6 cm. Fir density in this stand was very low (1–3 trees·ha⁻¹) but dominated the largest diameter classes up to 123.4 cm DBH and contributed over 25 % of the total stand basal area (13.9 m²·ha⁻¹ of 50.4 m²·ha⁻¹; Table 2). In contrast, in Lizardoia where fir was more abundant, the species appeared in all DBH classes and dominated the smallest size class (170 trees·ha⁻¹). There, the proportions of beech and fir were similar for the mid-size classes (20 cm – 50 cm), whereas beech dominated in larger DBH classes. Aboveground biomass (AGB) was higher in Lizardoia but more variable between plots than in Aztaparreta (Fig. 2). In both forests, beech represented the largest proportion of AGB (58–100 %).

In Lizardoia, beech was significantly larger (37.8 cm vs 51.7 cm; $F = 27.29$, $p < 0.001$) and taller (23.7 m vs 31.0 m; $F = 55.18$, $p < 0.001$) than fir, while in Aztaparreta fir was taller and larger than beech (Table 1; Figure SM1). Beech was taller in Lizardoia than in Aztaparreta (31.8 m vs 25.8 m; $F = 67.44$, $p < 0.001$) but had only marginally larger DBH (51.7 cm vs 47.5 cm; $F = 3.807$, $p = 0.0519$). Fir in Aztaparreta was taller (33.5 m vs 23.7 m; $F = 23.69$, $p < 0.001$) and had larger DBH (83.4 cm vs 37.8 cm; $F = 119.9$, $p < 0.001$) than in Lizardoia (Table 1; Figure SM1). These interspecific differences were observed also among plots within each reserve (Figure SM2). Fir also maintained larger live crowns than beech (Figure SM3). Trees of the two species were on average older in Aztaparreta than in Lizardoia (252.5 years vs 170.7 years; $F = 45.63$, $p < 0.001$) and beech was older than fir in both stands (maximum ages of 459 years and 378 years for beech vs 287 years and 218 years for fir) (Table 1; Figure SM1). In the old-growth forest Aztaparreta, tree diameter and age diversity were larger than in Lizardoia, but height diversity was lower (Figure SM2).

In Aztaparreta, beech in 2018 showed a similar DBH distribution to that of the old-growth section of the reserve surveyed in 1988 (Fig. 2) characterized by low stem density (minimum sampling threshold in 1988 was DBH ≥ 17.5 cm) with either a dominance of large trees or presence of trees across a wide DBH range (Gil Pelegrín et al., 1989). In both surveying years, the forest had a rather flat distribution of trees across the DBH classes.

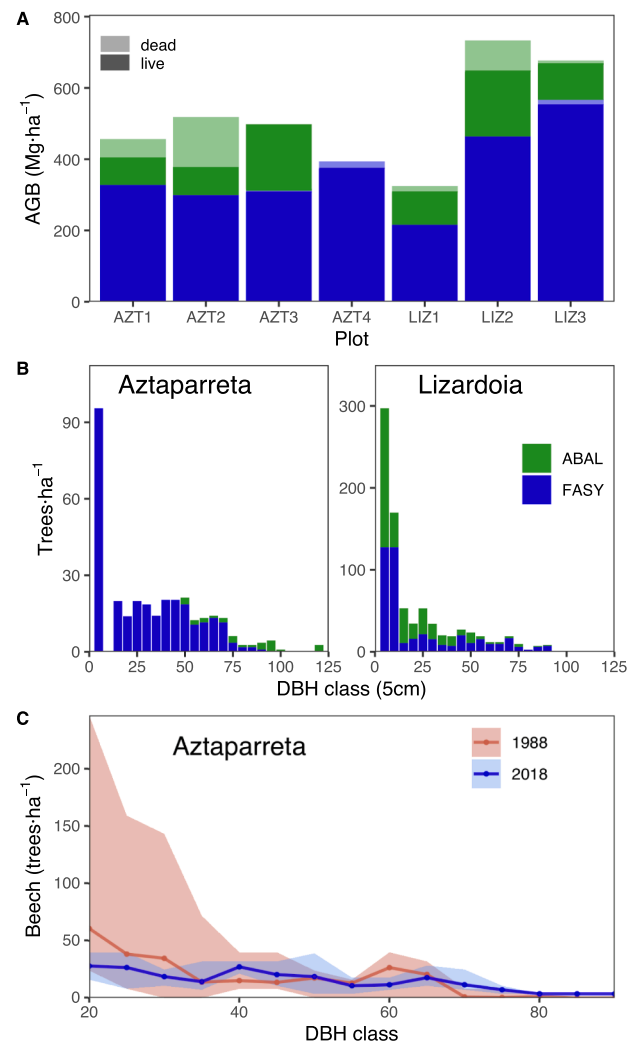


Fig. 2. Structural characteristics of the two study reserves. (A) Above ground biomass (AGB, Mg·ha⁻¹) for each plot. Darker colors show live AGB and lighter colours dead AGB. (B) Distribution of diameter at breast height (DBH) at reserve scale. Note different y-axis scales for each reserve. (C) Comparison between DBH distribution of beech trees (DBH ≥ 20 cm) in Aztaparreta in 1988 (Gil Pelegrín et al 1989) and 2018. Lines represent mean values and shaded areas the total range of data. Note that data for 1988 and 2018 followed different sampling schemes.

3.2. Long-term growth and aboveground biomass dynamics of beech and fir

In Aztaparreta, the mean growth of individual silver fir trees was several orders of magnitude higher than that of beech, although with high variability (Figure SM4). Faster silver fir growth persisted for over 100 years (AZT3) and up to several centuries (AZT1 and AZT2). At the stand level, however, the low abundance of silver fir in AZT1 and AZT2 resulted in much lower growth than in beech (Fig. 3). In AZT3, the presence of young, fast growing silver fir resulted in similar AGB increments for both species over the last century (Figure SM4). In contrast, in Lizardoia, mean tree-level growth was similar for beech and silver fir. For the last few decades, stand-level growth was also similar for both species in two of the plots. In the only plot in Aztaparreta with no fir (AZT4), total beech AGB was higher than in the other three plots, but total AGB was lower than in mixed plots (Table 2; Fig. 2). Similarly, total annual AGB increments (AGBI) in mixed plots was higher than in the only pure beech plot, with similar beech AGBI (Fig. 3).

Table 2
Summary description of the two forest reserves from the seven plots analysed.

Site	Plot	Stem density (trees·ha ⁻¹)			Basal area (m ² ·ha ⁻¹)			AGB total (Mg·ha ⁻¹)			AGB dead (Mg·ha ⁻¹)		
		ABAL ^b	FASY ^b	Total	ABAL	FASY	Total	ABAL	FASY	Total	ABAL	FASY	Total
Aztaparreta (AZT)	AZT1	35.4	314.8	350.0	14.7	35.9	50.6	129.2	327.4	456.6	51.7	0	51.7
	AZT2	38.9	187.4	226.0	20.7	32.5	53.2	219.3	298.9	518.2	139.7	0	140.0
	AZT3	21.2	267.9	289.0	20.0	35.4	55.4	185.7	312.4	498.1	0	2.8	2.8
	AZT4	0	413.8	414.0	0	42.3	42.3	0	394.5	394.5	0	18.3	18.3
	Stand mean	23.9	296.0	319.8	13.9	36.5	50.4	133.6	333.3	466.8	47.9	5.3	53.2
Aztaparreta (AZT 1998) ^a	Stand	9.8	255.6	265.4	6.5	28.9	35.5	78.3	243.4	321.7	n.a. ^c	n.a.	n.a.
Lizardoia (LIZ)	LIZ1	789.6	983.2	1773.0	17.1	26.2	43.3	108.5	215.7	324.2	14.6	0	14.6
	LIZ2	170.6	123.8	294.0	30.0	46.8	76.8	269.7	463.7	733.4	84.4	0	84.4
	LIZ3	195.4	203.4	399.0	16.7	57.4	74.1	110.2	566.1	676.3	6.3	11.4	17.7
	Stand mean	385.2	436.8	822.0	21.3	43.5	64.7	162.8	415.2	578.0	35.1	3.8	38.9

^a, data from 47 plots with 1256 m² in size where trees with DBH ≥ 17.5 cm were inventoried (Gil Pelegrín et al., 1989).

^b, species codes are: ABAL (*Abies alba*) and FASY (*Fagus sylvatica*).

^c, not available (missing information).

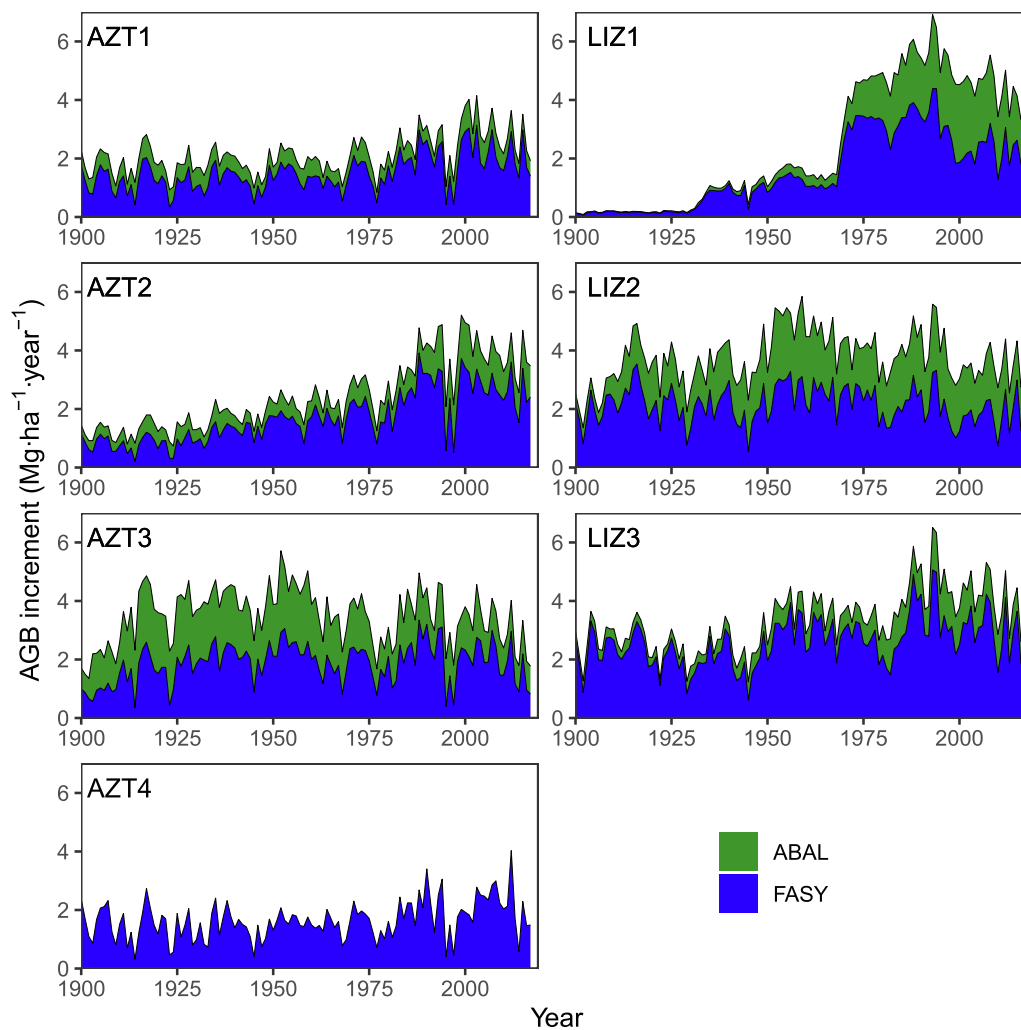


Fig. 3. Total aboveground biomass increment (AGB increment; in Mg·ha⁻¹·year⁻¹) for each plot in the two study forests for the period 1900–2017. Only trees present at the time of sampling (2018) were considered.

3.3. Disturbance and recruitment dynamics

For several centuries, both forests experienced small, frequent disturbances affecting less than 10 % of the trees present at that time (Fig. 4A). Several larger disturbance episodes affected 20 % or more in Aztaparreta around 1725, 1825, 1880, and 1975 while Lizardoia experienced a long period of higher disturbance between 1700

and 1780 and a shorter one around 1950. Lizardoia was characterized by a long period of low disturbance (<20 % of trees released) between the late 1780s and 1920s. Temporal occurrence of these larger disturbance episodes was not synchronous in both stands; only the event in 1825 appeared in both stands. Within-site disturbances was rather synchronic among plots in Aztaparreta but not in Lizardoia (Figure SM5).

Similar to disturbances, recruitment dynamics differed between

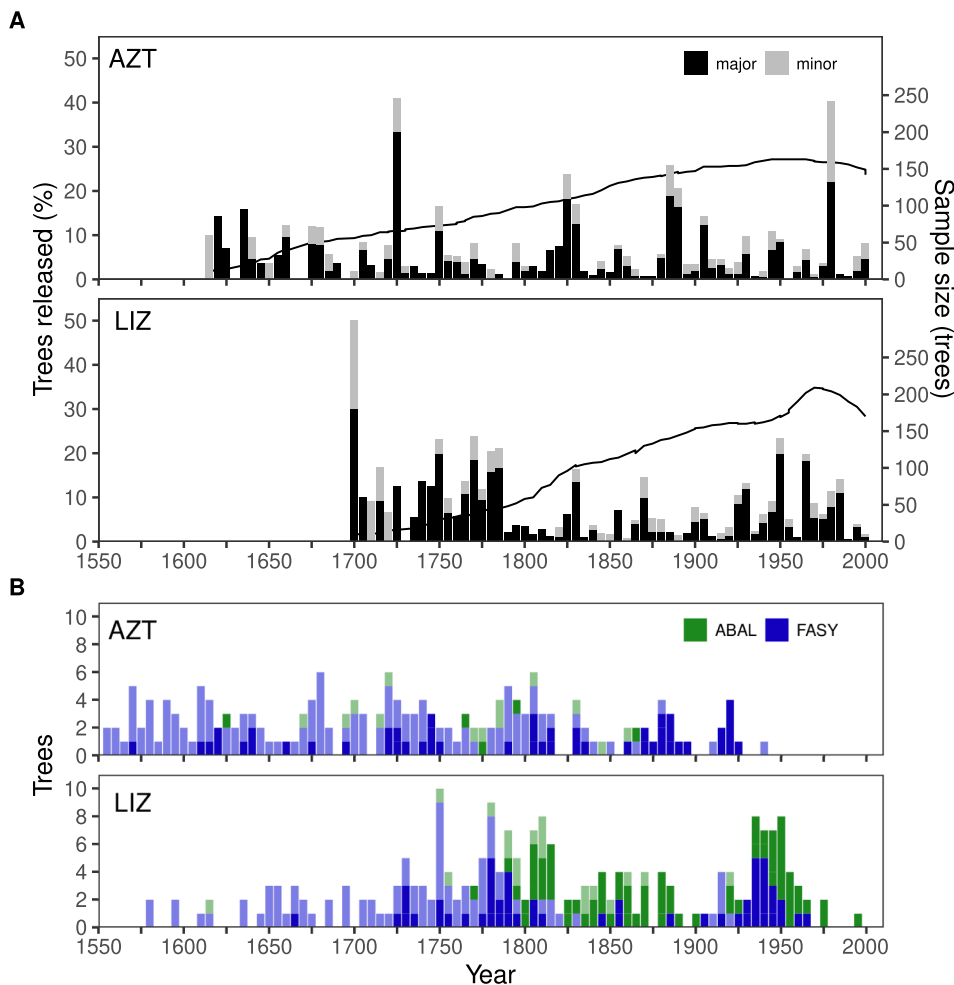


Fig. 4. Release and recruitment dynamics in the two study reserves. (A) Percentage of trees showing major and moderate radial growth releases per decade. Data were truncated for the period with 5 or more trees. Black lines show the total number of trees sampled in each reserve. (B) Recruitment of trees (i.e. time when they reach breast height) of each species through time. Darker colours show trees for which pith was reached or it was estimated to be < 10 years of the last ring dated, whereas lighter colours show trees for which the last ring was estimated to be > 10 years from the pith.

forests both in time and pattern (Fig. 4B). Recruitment in Aztaparreta was more homogenous with few larger recruitment episodes and similar among plots. In contrast, Lizardoia showed three recruitment events (1775–1790, 1800–1820 and 1930–1970) corresponding to asynchronous recruitment in plots (Figure SM6). Beech recruited mainly during two periods 1725–1800 and 1925–1950. Fir recruited almost continuously since 1780 with higher recruitment between 1780 and 1880 and between 1925 and 1970 (Fig. 4B; Figure SM6). These peaks of fir recruitment in Lizardoia followed peaks of beech recruitment by 5–15 years which in turn followed periods of increased disturbance.

Although both forests were uneven-aged structured, different recruitment dynamics resulted in large differences in ages at 1.3 m above ground level between stands (Fig. 5). In Aztaparreta, trees were evenly distributed across age classes, many trees were 400 years old or older and a few were younger than 200 years. In contrast, in Lizardoia young beech and fir trees (<100 years old) were frequent, but trees > 400 years old were rare. The asynchronous recruitment of the two species resulted in complementary age distributions: fir dominated the 100–210-year old range while beech dominated between 220 and 380 years old. Within young trees (<100 years old), fir trees were generally younger than beech trees (Fig. 5).

3.4. Simulation results and comparisons with stand data and disturbance histories

Results from ForClim simulations generally reflected well the total forest basal areas and composition of our study sites (Fig. 6). We present basal area instead of above ground biomass (AGB) because basal area

does not depend on specific allometric equations used, but AGB showed similar patterns. The model simulated basal areas within the range of observations including the higher basal area observed in long-untouched Lizardoia than in the old-growth Aztaparreta. Model simulations reflected the great dominance of *F. sylvatica* over any other tree species in these forests. Model simulations represented well observations in the old-growth forest Aztaparreta for both species both in 2018 and at forest scale in 1988 (Fig. 6). In the long-untouched forest Lizardoia, ForClim simulated lower basal areas of silver fir than our observed basal areas in 2018. In both forests, simulations overestimated the abundance of less shade-tolerant tree species, mainly maples (*Acer* sp.), *Quercus petraea* and *Pinus sylvestris*. The main climatic limiting factors for the simulated regeneration of *A. alba* in these forests were warm winter minimum temperatures, particularly for the warmer site Lizardoia, and browsing, which affected both sites similarly (Table SM1). Climate or browsing had lower effects on beech regeneration. The model showed no limitation due to drought stress for the establishment (Table SM1) or growth (Table SM2) of any species under current climate. Growth of beech and fir were mainly limited by available light and growing degree days (Table SM2).

Our comparison between empirically-derived forest productivity (annual AGB increment) and productivity simulated by ForClim again showed higher agreement for beech than for fir and for the old-growth site Aztaparreta than for the long-untouched Lizardoia (Fig. 7). ForClim correctly simulated higher beech productivity in Lizardoia than in Aztaparreta, but overestimated productivity for silver fir in both forests. Increased productivity of surviving trees or newly recruited trees after disturbance events at both sites induced high variability of empirical

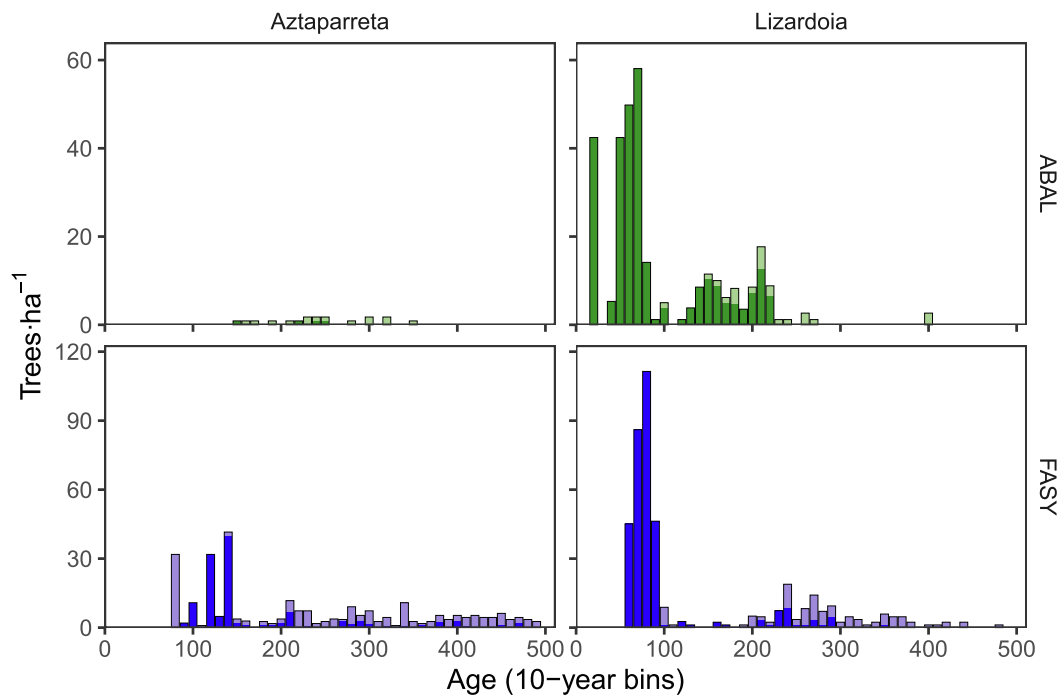


Fig. 5. Distribution of tree ages at breast height for *Abies alba* (ABAL) and *Fagus sylvatica* (FASY) in the two study reserves. Tree ages are binned in 10-year wide classes. Note different y-axis scales for each species to allow detail. Darker colours show trees for which pith was reached or it was estimated to be ≤ 10 years of the last ring dated, whereas lighter colours show trees for which the last ring was estimated to be > 10 years from the pith.

productivity between plots (Fig. 5). This increased variability was particularly high in fir for the most recent disturbance events, which caused fir productivity to exceed the ranges of productivity simulated by ForClim. Within a few decades of these disturbance events, empirical productivity of fir was again within the ranges of simulated productivity, with the exception of Lizardoia.

4. Discussion

Structural characteristics of the two reserves confirmed the common belief of their conservation status based on historical accounts (Viers, 1955). Stand structure characteristics in basal area, stand density, and high presence of large living trees (DBH > 50 cm) in old-growth Aztaparreta was similar to those of other old-growth temperate forests in Europe (Burrascano et al., 2013) and North America (Halpin and Lorimer, 2016). Lizardoia with higher stand density and basal area, lower age and fewer large trees, and a negative exponential DBH distribution showed characteristics of long-untouched forests. However, these characteristics also resemble structural characteristics of old-growth forest with more recent and intense natural disturbances and the natural range of structural diversity in old-growth forests (Nagel et al., 2006; Trotsiuk et al., 2012; Halpin and Lorimer, 2016). Although old-growth and long-untouched forests may show similar structural features (Horvat et al., 2018) at some point in time, reconstruction of disturbance histories adds substantial information to understand forest naturalness and conservation status (Di Filippo et al., 2016), and biomass accumulation dynamics (Molina-Valero et al., 2021).

4.1. Disturbance regime and recruitment dynamics in mixed beech-fir forests

Our reconstruction of past forest disturbance dynamics showed contrasting long-term forest development in the two forests with different developmental stages. The disturbance regime in the old-growth forest (Aztaparreta) during the last four centuries was characterized by frequent small-scale canopy disturbances combined with less

frequent medium-scale disturbances. Similar disturbance regimes dominated by gap dynamics are characteristic of temperate old-growth forests dominated by shade-tolerant species (Splechtina et al., 2005; Fraver et al., 2009; Trotsiuk et al., 2012; Martin-Benito et al., 2020) and where extensive windthrow damage may be attenuated by topography or forest structure (Fraver et al., 2020; Martin-Benito et al., 2020). In contrast, our analysis evidenced a long period (1700–1780) of sustained medium disturbance in the long-untouched forest consistent with human activities. Although dendroecological methods do not allow to definitely distinguish between logging and natural disturbances, historical accounts suggest that the reconstructed disturbance events during the 18th century were caused by logging (Viers, 1955; Aragón-Ruano and Riezu Elizalde, 2021). Our results of growth releases suggest that logging ceased around 1780 which is consistent with the date of the first attempt to protect this forest in the early 1780s (Aragón-Ruano, 2022). The abundant presence of trees that recruited previous to these logging episodes in all plots in Lizardoia (Figure SM6) suggest that logging was probably selective and that clear cutting can be ruled out as it would have removed all trees from the stand.

Complex interactions between different environmental variables drive tree regeneration and recruitment in mesic temperate forests and may affect seedlings and saplings differently. The lower disturbance levels in Aztaparreta created a continuous recruitment pattern through time compared to the temporally more clustered recruitment events in Lizardoia, which had a more intense disturbance regime. Fir and beech seedlings benefit from high level of shading under the canopy (Käber et al., 2021) allowing to build up abundant advanced regeneration of shade-tolerant species (Petrovska et al., 2021). Disturbance-induced gaps increase light availability and allow this advanced regeneration to recruit into larger trees (Hunziker and Brang, 2005; Nagel et al., 2006; Orman et al., 2021). Abundant fir and beech regeneration are commonly observed in gaps created by intense logging in nearby forests (Cabrera, 2001). Beech recruitment generally preceded that of fir by 5–15 years probably due to the faster height growth rates of beech saplings (Orman et al., 2021) allowing beech to reach sampling height several years before fir. Results from the DVM also showed increases in beech basal

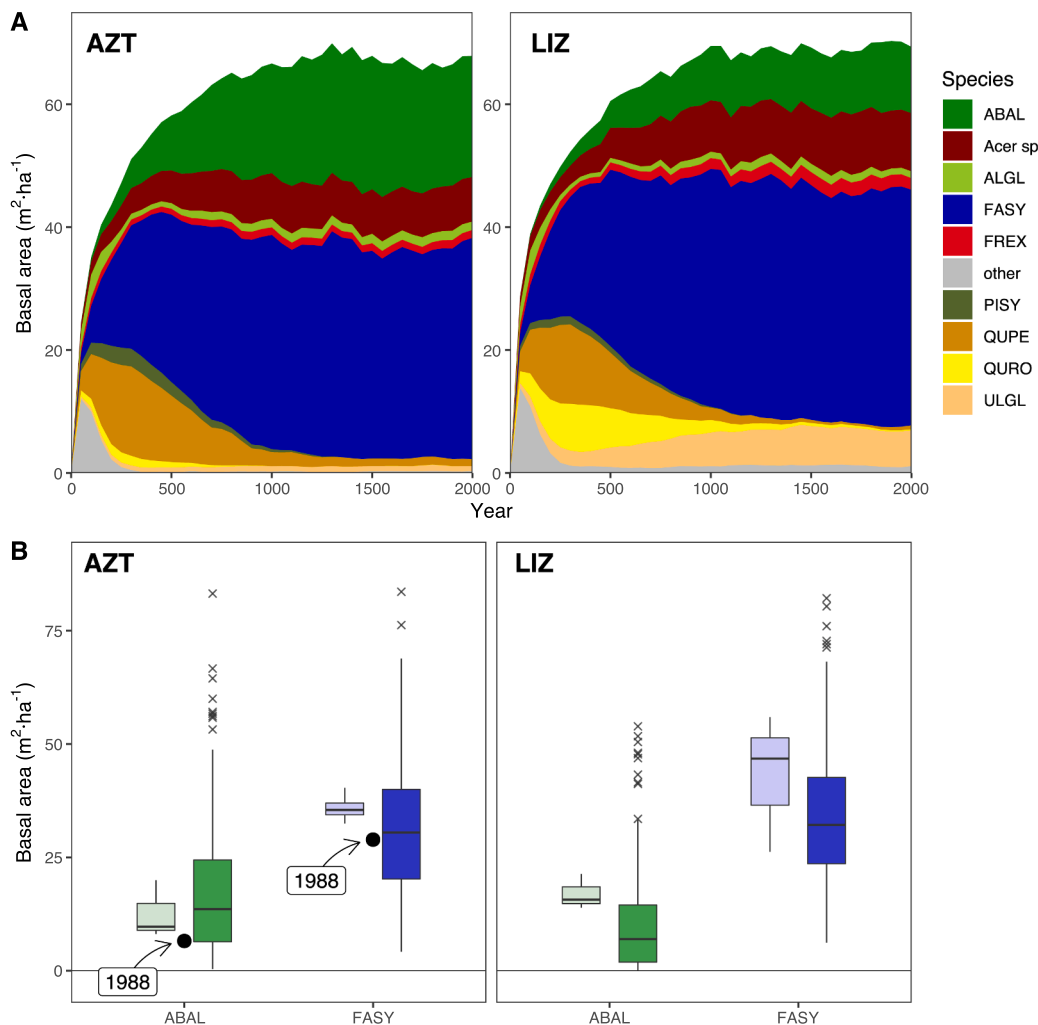


Fig. 6. (A) Simulated transient dynamics of basal area ($\text{m}^2\cdot\text{ha}^{-1}$) for the two study reserves starting from bare ground and run for 2000 years. Results are average basal area for 200 patches each 800 m^2 in size. Species acronyms: ABAL, *Abies alba*; ALGL, *Alnus glutinosa*; FASY, *Fagus sylvatica*; FREX, *Fraxinus excelsior*; PISY, *Pinus sylvestris*; QUPE, *Quercus petraea*; QURO, *Q. robur*; ULGL, *Ulmus glabra*. Species representing less than 1 % of basal area at any given time are combined and labelled as 'other'. (B) Comparison of observed (light colors) and simulated (dark colors) basal areas ($\text{m}^2\cdot\text{ha}^{-1}$) for each species at the end of 2000-year simulation periods when conditions represent equilibrium species composition at the ecosystem level. Simulated basal areas show results for 200 patches 800 m^2 in size. Crosses show outliers. For Aztaparreta (AZT), black dots show mean basal area observed in 1988 across the entire reserve (Gil Pelegrin et al 1989).

area preceding increases in fir. Although silver fir regeneration and recruitment may also be strongly limited by other environmental conditions like ungulate browsing (Ammer, 1996; Nagel et al., 2006; Caillet et al., 2014; Ameztegui and Coll, 2015), but ungulate densities would be similar in both forests.

Low rates of canopy disturbances in both forests over the last two hundred years allowed the dominance of long-lived, shade-tolerant beech and fir and the absence of less shade tolerant species consistent with results from temperate mixed forests in Europe and North America (Fraver et al., 2009; Nagel et al., 2014). More light-demanding species, such as *Acer* sp. and *Q. petraea*, are present in the vicinity of both stands (personal observation and Villar Pérez, 1980) but were absent from them. For example, the disturbance event resulting from logging in the 18th century in Lizardoia would have created gaps large enough to allow the recruitment of these less shade-tolerant species, but none that survived several centuries. Low disturbance regimes that allow profuse advanced regeneration of shade-tolerant species prevent the recruitment of less shade tolerant species even after large disturbance events (Fraver et al., 2009; Nagel et al., 2014). Single disturbance events may not be enough to increase the presence of less shade-tolerant species which may require more frequent medium to large disturbances under the

studied conditions.

Despite the low abundance of fir in the old-growth forest Aztaparreta (7.5 % of trees in the stand), it dominated the larger diameter classes, accounted for over 29 % of AGB and showed higher growth rates than beech. Thus, performance of adult fir trees at this site could be as good or better than beech and the low abundance of fir may be due to low recruitment, which could be caused by low disturbance rates. In contrast, in Lizardoia the stronger competition caused by its higher stem density induced lower growth rates of beech and fir. Preferential logging of fir for timber probably contributed to lower presence of the species at local and regional level favoring beech (Viers, 1955; Villar Pérez, 1980). During the understory re-initiation phase that followed after partial logging ceased (1780–1925), most trees recruiting and still present in the canopy in 2018 were silver fir. Fir may recruit into the canopy better in forest gaps (Cabrera, 2001; Horvat et al., 2018) and commonly declines later with stand age and forest succession (Horvat et al., 2018; Albrich et al., 2021) as observed for the old-growth forest Aztaparreta. More than two centuries without logging in the long-untouched forest may not be enough to erase the effects of previous human activities, so that centennial legacy effects from logging still affect secondary succession, composition and productivity in the forest landscape.

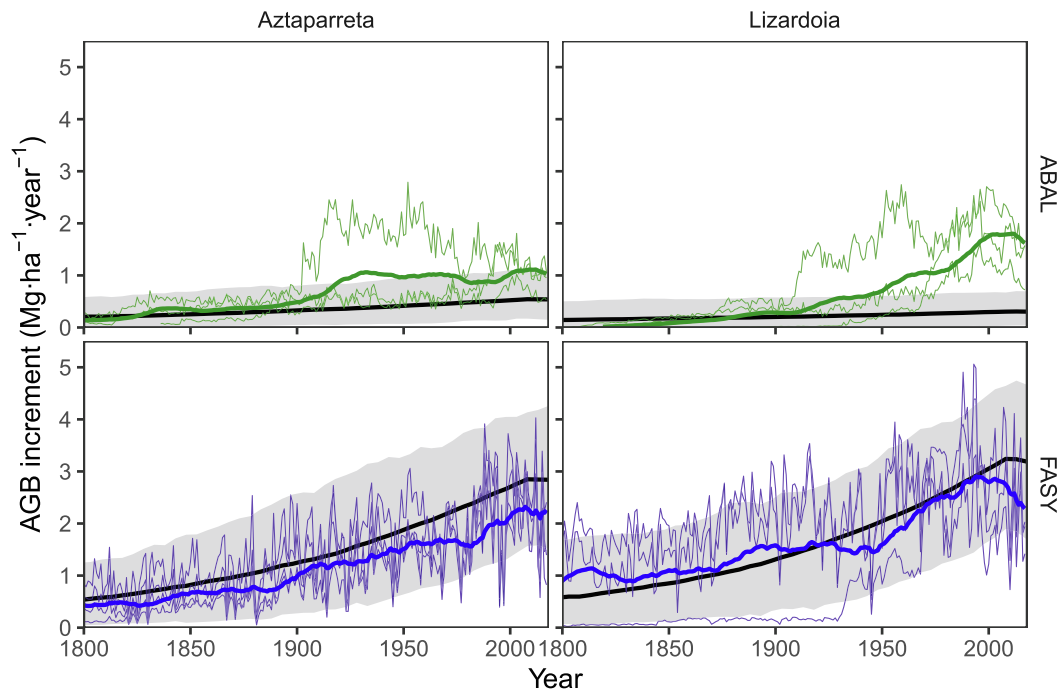


Fig. 7. Forest productivity (AGB increment) for *Abies alba* (ABAL) and *Fagus sylvatica* (FASY) in the two study forest reserves derived from dendroecological methods compared to productivity simulated by ForClim for each species. In each panel, green and blue lines represent productivity estimated per species by dendroecological methods for *A. alba* (green) and *F. sylvatica* (blue) with thin lines representing AGB increment at plot level for each species and thick lines representing the 20-year moving average for each forest reserve. Black lines represent the mean AGB simulated by ForClim and grey area around the mean represent the 5% and 95% percentiles for each species in the 200 patches simulated.

Although silver fir decline has been reported in our study area (Gil Pelegrín et al., 2008; Camarero et al., 2011), our results did not show any signs of decline at any of the forests analyzed. Silver fir decline increasing with heavier logging intensities was attributed to the fact that logging selected for larger trees while leaving small-diameter and slow-growing trees which would be more prone to die decades after (Gil Pelegrín et al., 2008; Camarero et al., 2011). ForClim simulated fir abundance and productivity similar to observations at the old-growth forest, but underestimated it at the long-untouched forest, suggesting an important positive effect of past logging on silver fir. Our results thus suggest that past logging in the long-untouched forest would have contributed to increasing fir productivity and abundance outside its natural range, particularly on its southern and lower distributional limits. Silver fir decline in the area may be partly considered as the natural successional process acting over previous compositional changes (Horvat et al., 2018; Albrich et al., 2021) resulting from land-use legacies.

The fact that fir growth increased total plot growth and that fir presence did not reduce beech growth (Figs. 2 and 3) suggests positive complementarity in stand-level growth (Mina et al., 2018; Schwarz and Bausch, 2019) which is in line with the commonly higher productivity in mixed stands than in monospecific stands (Morin et al., 2011). In mixed beech-fir forests with low or no drought stress (Linares and Camarero, 2012), competition for light may be a more limiting factor than competition for underground resources as shown by our model simulations (Table SM2). Differences in live crown architecture between the two species suggest structural canopy stratification and complementarity, more efficient use of light in the canopy allowing for faster total stand-level growth than in monospecific stands. Asynchrony in species recruitment evidenced in Lizardoia would also suggest successional effects on positive complementarity (Mina et al., 2017). Although higher structural diversity in canopy structure may promote forest productivity (Glatthorn et al., 2017), measured and simulated aboveground biomass (AGB) and AGB growth were lower in the old-growth forest, as reported

for a larger dataset of beech-fir forests in the Pyrenees (including our plots) (Molina-Valero et al., 2021) and the Alps (Albrich et al., 2021). In fact, site maximum AGB and productivity may be generally reached at intermediate phases of succession rather than at the old-growth forest phase (Bormann and Likens, 1979; Molina-Valero et al., 2021).

4.2. Benchmarking a DVM with empirical structure, composition and productivity

The old-growth Aztaparreta reserve showed little changes between 1988 and 2018. Only one third of the plots sampled in 1988 (Gil Pelegrín et al., 1989) showed higher abundance of smaller trees than our 2018 data, despite differences in sampling methods. Similar differences were observed between dendroecological plots and large plot inventories in other old-growth beech forests (Trotsiuk et al., 2012). A closer agreement between results of DVM simulations, mainly of beech which was the dominant species at the site, and the reserve-wide 1988 inventory than with our inventory of selected fully-stocked stands was expected because simulations include plots with a larger range of developmental stages than our sampling plots. In general, our results showed that the model performed well for both forests. Closer agreement between DVM simulations and empirical inventories in the old-growth forest could add further evidence that this forest represents better the potential natural vegetation under dynamic equilibrium at mid-elevations of the western Pyrenees. By contrast, logging over 200 years ago in the long-untouched forest increased recruitment of both beech and fir. More disturbances, however, did not promote the existence of less shade tolerant species as opposed to our ForClim simulations and other old-growth forests in Europe (Nagel et al., 2014) or they may have gradually disappeared from our stands as succession progressed. Comparing empirical forest data with simulation results showed that forest conditions resulting after such logging events may have affected post-disturbance forest development including forest responses to subsequent disturbances (Stritih et al., 2021). These long-term legacies affect current ecosystem

dynamics and may modify forest resilience to climate change (Thom et al., 2018), and delay the recovery of old-growth conditions. Our results highlight the potential of benchmarking DVM simulations with long-term empirical data to better understand the complexity of forest dynamics and their response to future climate changes.

5. Conclusion

In the western Pyrenees, species composition in mixed beech-fir forests appeared to be conditioned by disturbance frequency and intensity. Within the disturbance regimes analyzed, fir proportion increased with disturbances. With a less severe disturbance regime, fir abundance gradually decreased but maintained biomass accumulation in the old-growth forest. Thus, species dominance in these forests alternates between beech and fir conditioned by disturbance intensity and frequency. Within the range of disturbance intensity analyzed, the high shade tolerance of beech and fir reduces the presence of more light-demanding species such as oaks or maples. Many forest structural attributes converge to those of old-growth forests but important legacy effects from logging may remain in the landscape for several centuries, including species composition, structure, and productivity. At regional scales, the combination of old-growth forests with long-untouched forests and forests managed by uneven-aged practices that create structural heterogeneity at different spatial scales may contribute to create a landscape-level mosaic and maintain different mixtures of beech and fir.

CRedit authorship contribution statement

Dario Martin-Benito: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing - Original draft preparation. **Juan Alberto Molina-Valero:** Investigation, Data curation, Writing - Review & Editing. **César Pérez-Cruzado:** Investigation, Data curation, Writing - Review & Editing. **Christof Bigler:** Writing - review & editing. **Harald Bugmann:** Methodology, Writing - review & editing.

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.

Data availability

All wood core samples are permanently archived at INIA-CSIC (Madrid, Spain) and are available for non-destructive research purposes from the corresponding author on reasonable request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120541>.

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