



The Renaissance of Mixed Forests? New Insights Into Shifts in Tree Dominance and Composition Following Centuries of Human- induced Simplification of Iberian Forests

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ABSTRACT

Anthropic activities have modelled and simplified southern European forest landscapes for centuries. Over recent decades, new drivers related to human-mediated global change have induced the redistribution of tree species and an increase in more complex forests. However, the current large-scale patterns and drivers of these changes are yet to be fully described for the Mediterranean Basin. In this frame, this work identifies and examines changes in dominance and composition from pure to mixed forests across bioclimatic gradients and forest types in Iberian forests over recent decades based on data from the Spanish National Forest

Inventory from 1960 to 2020. Then, considering different environmental, anthropic, and disturbance variables we also identify some of the most important drivers associated with the shifts observed from 1986 to 2020. Our results confirm an ongoing increase in mixed forests involving the replacement of conifers by broadleaved species. These shifts are greater in the Atlantic biogeoregion and in pure broadleaved deciduous forests. Climate warming-associated disturbances such as drought severity together with land use legacies and forest types showed the strongest relationships with the observed changes in the studied forests. Our results support the premise put forward by palaeoecologists which states that the increase in tree mixtures is a natural process reversing the historical human-induced simplification of Iberian forests. The increasing importance of mixed forest in southern Europe makes decisive the revision of forest classifications as well as forest management and conservation plans in order to include these increasingly abundant novel stands in forest policies.

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Key words: Anthropocene; Biogeography; Dominance and compositional shifts; Global change; Mixed forests; Non-native species.

HIGHLIGHTS

- There is an ongoing shift from pure to mixed forests in southern Europe
- Shifts are greater in deciduous forest. Conifers are being replaced by broadleaves
- Shifts are mainly associated with climate warming effects and land use legacies

INTRODUCTION

The Anthropocene is leading to the reorganization of natural communities worldwide. Although the distribution of vegetation is largely controlled by climate and by geographical dispersal limitation (Svenning and Skov 2005), in the Iberian Peninsula, historical and recent human disturbance has been cited as the main cause of vegetation change for at least the last 4500 years (Valbuena-Carabaña and others 2010). Anthropogenic legacies have progressively modelled and simplified forest landscapes in the Iberian Peninsula since the Pleistocene (Morla-Juaristi and others 1990). Factors such as historical land use for agriculture, grazing pressure, human use of fire and tree species selection have led to a reduction not only in the extent of woodlands but also in the structural and compositional diversity of forests in the Iberian Peninsula (for example, Blondel 2006; Connor and others 2021). Thus, while palaeoecological records point to the existence of wide areas of inland Spain covered by mixed forests during the Holocene (Carrión and others 2000; Morales-Molino and others 2017), according to the FAO (2020) and Forest Europe (2020), the main forest types found in the Iberian Peninsula today are pure or monospecific forests (i.e. forests where the canopy cover of the dominant species is greater than 70–90% of the total tree crown cover depending on the reference definition (Schuck and others 2002; Bravo-Oviedo and others 2014)).

Since the second half of the twentieth century, the European continent has undergone a transition from a net loss to a net increase in forest cover (Kauppi and others 2018; FAO 2020; Forest Europe 2020). In Spain, this net increase in forests has resulted from a combination of large-scale refor-

estation and afforestation plans since the beginning of the last century; together with the application of the Common Agricultural Policy (CAP), which promoted the conversion of agricultural land to forest land in the 1990s; and spontaneous forest regrowth following the widespread abandonment of traditional land uses, particularly since the 1960s (Vadell and others 2016; Martín-Forés and others 2021).

Recent research on Iberian forests shows anthropogenic-driven rapid shifts in tree species distribution (Urli and others 2014; Hernández and others 2014) concomitant with changes in tree species dominance and composition (Urbieta and others 2011; Vayreda, and others 2013, 2016; Sánchez de Dios and others 2016). In addition, mismatches and limitations between adults and recruitment and forest succession along environmental gradients have been also described in previous works (Vilá-Cabrera and others 2012; Carnicer and others 2013, 2014; Benavides and others 2015; Hernández and others 2019). As a result of tree species redistribution, these studies show an enlargement of ecotonal vegetation belts (Hernández and others 2017) and new species interactions (Gómez-Aparicio and others 2011). However, despite all these efforts, the current large-scale patterns and drivers of changes in forest dominance and composition are yet to be fully described for the Mediterranean Basin. For that, additional global change drivers such as land use changes and climate warming-related disturbances (wildfire occurrences and droughts) also need to be considered (Vayreda and others 2016). This is of great importance for forest management and conservation practices over the coming decades. It is necessary to determine the contexts and conditions under which, not only biotic and abiotic factors but also anthropic factors mediate species redistribution, and to what degree those factors determine these contemporary forests (Sheffer 2012; Lenoir and Svenning 2015; Pecl and others 2017; Pyšek and others 2020).

In this work, we aim to shed light on this subject by studying in detail the large-scale patterns of shifts in dominance and composition in Iberian forests. Based on data from the Spanish Forest Inventory from 1960 to 2020, we firstly assess whether changes in forest tree species dominance are leading to a shift from pure to mixed forest. Secondly, we examine the compositional shifts from pure to mixed forests by forest types and biogeographical regions considering the re-measured SFI plots (1986–2020). Finally, using different environmental, anthropic, and disturbance

variables, we identify factors associated with the shifts in dominance and composition from pure to mixed forests in this last studied period (1986–2020).

The depiction and study of drivers of contemporary mixed forests will allow us to understand whether they are historical systems (*sensu* Landres and others 1999), novel ecosystems (*sensu* Hobbs and others 2006) or hybrids. Furthermore, in a context of potential limited adjustment of Iberian forests to contemporary climate warming drivers, such as increasing fire regimes and more frequent extreme climatic events like droughts, it is crucial to understand the implications of these shifts for future forest functioning and ecosystem services (Morin and others 2011; Garcia-Valdés and others 2020).

Palaeoecological records reveal that mixed forests have played a more important role in forest landscapes of the Iberian Peninsula in the past. Our hypothesis is that we are witnessing a process reversing the historical human-induced simplification of forests and the rise or renaissance of more complex forest mixtures. Our goal is therefore to demonstrate the increase in mixed forest over the last decades and make a connection to human legacies in forests. Future perspectives and new actors derived from global change which add complexity and uncertainty to this process are discussed.

MATERIAL AND METHODS

Study Area

The study area covers the entire climatic gradient of Spanish forests in the Iberian Peninsula, from the Atlantic and Alpine bioregions in northern Spain to more Mediterranean conditions in Central and Southern Spain, with mean annual temperatures ranging from 2 to 18 °C and annual precipitations from 290 to 1950 mm (Figure 1). This wide climatic gradient together with the diversity of the topography and soil types of Iberian Spain results in a broad range of natural forest types from sclerophyllous and drought adapted forests like holm oak (*Quercus ilex* L.) and stone pine (*Pinus pinea* L.) forests to alpine conifer and broadleaved temperate forests such as mountain pine (*Pinus uncinata* Ram.) and European beech (*Fagus sylvatica* L.) forests that can be found in Central Europe (Costa and others 1997).

Study Variables

Spanish National Forest Inventory and SFI Plots Classification

To analyse changes in dominance and composition of Spanish forests over recent decades, the available forest information from the Spanish National Forest Inventory (SFI) was used. Although the SFI was first conducted in the 1960's (SFI1), it was not until SFI2 (1986) that it was designed as a systematic and continuous sample of concentric circular plots distributed throughout the forest-covered land of Spain on a 1-km square grid. Thus, since SFI2, the plots have been re-measured at an interval of approximately 10 years (Alberdi and others 2017) up to the most recent, ongoing cycle (SFI4). Each SFI plot is composed of four circular subplots with the same centre but different radii (5, 10, 15 and 25 m) and in which living trees with different minimum diameter thresholds are measured (7.5, 12.5, 22.5 and 42.5 cm, respectively). Species identification, diameter at breast height (dbh) and total tree height (h) are recorded in each plot for each sample tree over 7.5 cm. Additionally, in the 5-m radius plot, trees with dbh 2.5–7.5 cm are also identified and counted and their mean height is estimated.

To differentiate and classify pure and mixed SFI plots we adopted the current national definition used in international statistics such as Forest Europe (2020). When the basal area of a tree species was greater than 75% of the plot basal area, then the plot was classified as pure forest. If the basal area of all the tree species of the plot was less than 75% of total basal area, then the plot was classified as mixed forest.

The analysis of the changes in both tree dominance and composition of the SFI plots was extended still further by applying the previous classification of monospecific or mixed forests but this time considering the total basal area per plot of the following forest types: coniferous (PCON), broadleaved deciduous (PBDECID), broadleaved evergreen (PBEVERG) and broadleaved marcescent (PBMARC). In the case of mixed broadleaved forest classification, the more dominant type found defines the forest type (MCON, MBDECID, MBEVERG, MBMARC and MCONBROAD) (Supplement 1). Finally, as a proxy of the potential future changes in the composition and dominance of Iberian forests (FUT_PERS), this same classification was performed, considering the density of trees with dbh 2.5–7.5 cm, which represent the established regeneration or the juvenile forest stratum.

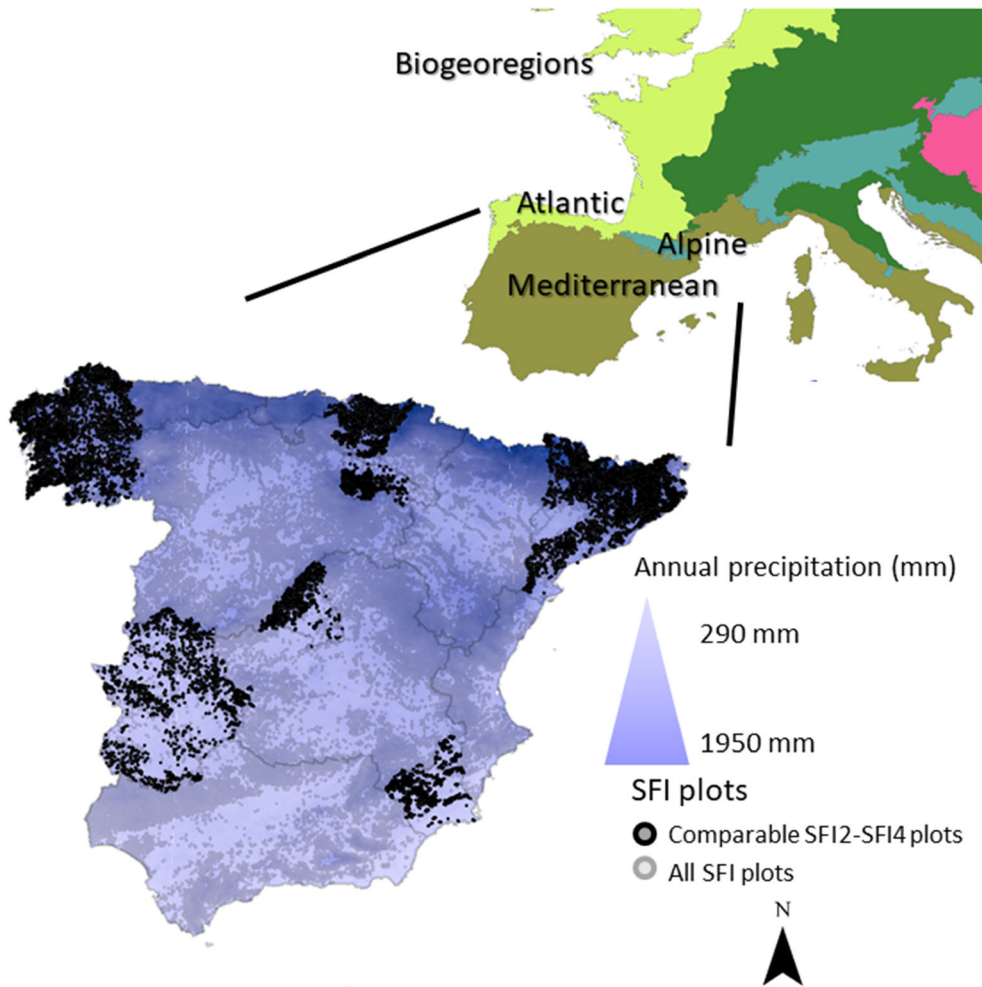


Figure 1. Location of Iberian Peninsula in SW Europe and the distribution of the three biogeoregions. The distribution of permanent SFI plots from SFI2 to SFI4 cycles is shown in black. The distribution of the rest of SFI plots in grey. The gradient of annual precipitation (mm) along Spain is also shown.

Considering the long-term dynamics of forests and to ensure the stability and consistency of the results this proxy was estimated from SFI2 to SFI4.

Data Analysis

First, we compiled percentages of SFI plots classified as pure and mixed forest from all SFI cycles to date, i.e. from SFI1 (1960) to SFI4 (2020), covering 60 years. Thus, we computed general statistics for the longest temporal series available.

Then, to further investigate shifts in tree dominance and composition as well as the factors associated with those changes, we focused the analysis at plot level in the regions with continuous SFI cycles available. We compared the information from 39,621 permanent SFI plots from the SFI2 (1986–1996), SFI3 (1997–2007) and SFI4 (2008–2020) cycles (Figure 1), covering a time interval of

approximately 30 years. In this SFI plot set, and to examine exclusively natural forest succession, we combined cartographical and baseline SFI cycle (SFI2 or SFI3 depending of the region) information in order to discard those permanent plots in which there were signs of intensive forest management or high level of anthropic intervention, i.e. monoculture plantations and *dehesa* woodlands. Using geographical information system (GIS) software QGIS 3.0.2 (QGIS Development team 2021) we overlaid baseline SFI plots with the Spanish Forest Map (MFE50 2006). We also use the GIS-Forest platform (García del Barrio and others 2009) to classify SFI plots as monoculture plantations and *dehesa* woodlands. In the end, we also considered intensive management stands to be those SFI plots where commercial non-native species such as *Eucalyptus* sp. and *Pinus radiata* D.Don were dominant. The final subsample analysed consisted of

36,684 SFI plots, all of them subject to different levels of management depending on land ownership and law regulations.

Finally, in the last step, we selected those plots in which a shift from pure to mixed forests between two continuous SFI cycles was identified (9,861 plots). Then, we examined the compositional shifts from pure to mixed forests by forest types as well as by biogeographical regions. For this, based on their location, we assigned each SFI plot to one of three different biogeographical regions present in mainland Spain: Alpine (ALP; 646 plots), Atlantic (ATL; 2,528 plots) and Mediterranean (MED; 6,687 plots) according to the European Environment Agency (EEA 2011). Factors associated with the shifts found were also described.

To analyse the relative importance of factors associated with changes in tree species dominance and composition within SFI plots over recent decades, both biotic and abiotic predictors were considered as independent variables in different analyses (Supplement 2). In relation to biotic factors, we might expect some variations in the change from pure to mixed stands depending on the type of forest. Furthermore, since previous studies have appointed biological invasions as main drivers of ecosystems changes (Lopez and others 2022), the presence of non-native tree species might as well have considerable effect in the change from pure to mixed forests. Therefore, the previously mentioned classification of monospecific forest types (FOR_TYPE) as well as two more factors regarding the presence/absence of non-native trees in each plot (ALOC) and the increment in non-native trees presence between SFI cycles (IN-ALOC) were considered.

As regards abiotic factors both physical (physiographic and climatic) and climate warming-related disturbance predictors were calculated. Slope (SLOP) is related to mountain areas where change in tree species dominance has been already reported due to land use abandonment (Ameztegui and others 2021). Aspect (ASP) and distance to the coast (DCOAST) are related to microclimate conditions that may act as drivers of change in the tree species composition (Chen and others 1999). The three of them were taken from the digital elevation model of Spain with a spatial resolution of 25 m (CNIG 2021). For climate characterization, we interpolated climate data for SFI plots from the WordClim 2.0 database (Fick and Hijmans 2017) with a 30 arcseconds (approx. 1 km) resolution. Climatic variables to be explored were selected based on physical characteristics generally being represented for the period 1985–2017: annual

mean temperature (AMT), annual precipitation (AP), mean temperature of the coldest quarter (MTCQ) (at Spanish latitude December, January and February), mean temperature of the warmest quarter (MTWQ) (at Spanish latitude June, July and August), and precipitation of the warmest quarter (PWQ).

Regarding climate warming-related disturbance variables, for each SFI plot drought and fire events were calculated. Both have been appointed as drivers of post-disturbance reorganization of forests (see, for example, Batllori and others 2020; Seidl and Turner 2022). For drought events, the Standardised Precipitation Evapotranspiration Index (SPEI 2.7, <http://hdl.handle.net/10261/268088>) was used as an indicator of hydrological drought events. The SPEI is a multi-scale drought index calculated from the monthly difference between precipitation and PET, with a spatial resolution of 0.5° (Vicente-Serrano and others 2010). The SPEI can be computed at different time scales because the SPEI value assigned to a particular month is calculated based on the averaged SPEI values of a time window covering the previous *n* months. SPEI values from 1985 to 2017 with a 6- or 12-month timescales were downloaded for each plot depending on the biogeographical region it belonged to. ALT regions located at more humid sites may present tree growth responses to mid-term droughts (6 months), while in ALP and MED regions at more semi-arid sites, trees may respond to long-term droughts (12 months) (Vicente-Serrano and others 2014). Drought periods were defined for SPEI values equal to or lower than -1 (Agnew 2000). Then, we computed four variables for the studied period, drought frequency as the number of drought events (F_DROUGHT), mean drought duration as the average duration of drought events (DUR_DROUGHT), mean drought intensity as the average of the mean SPEI values during drought events (INT_DROUGHT) and mean drought severity as the average of the accumulated SPEI values during drought events (SEV_DROUGHT) (Ashok and Vijay 2010; Palmero-Iniesta and others 2021).

Concerning wildfires, the variable frequency of fire (F_FIRE) was computed by adding the number of fires occurring in each SFI plot during the period 1996–2015. The information from the Spanish national statistics on forest fires is available in a digital map (MITECORD 2021a).

Finally, the plots were also classified according to their legal level of protection (MITECORD 2021b). Those plots located within any of the following legal protection figures were classified as protected (PROT): Natural Monuments, Nature Reserves,

Protected Landscapes, National Parks, areas protected by the Natura 2000 Network, other Protected areas. In addition, to consider the potential relationships between present and past human impact and the changes in dominance observed in SFI plots, we developed different indirect measurements of anthropic intervention. Because the abandonment of traditional land uses in the second half of the twentieth century was strongly tied to depopulation and to changes in economic structure (Lasanta 2002), the variables population change (CH_POPUL), population density (DENS_POPUL) and distance to the closest settlement (DIST_SETTL) were calculated to be considered as auxiliary variables (Ameztegui and others 2010). First, using the Spanish Geographic Database (IGN 2021), each SFI plot was assigned to one Municipality. Second, population figures from the SFI2 and SFI4 years (1986 and 2017, respectively) were consulted (INE 2021). Finally, CH_POPUL was calculated as the ratio between population in 2017 and 1986; DENS_POPUL as n° inhabitants/ha and DIST_SETTL as the distance (km) of each SFI plot from the closest settlement computed in QGIS.

To study the factors associated with shifts from pure to mixed forests, generalized linear models (GLM) with binomial error and logit link were constructed at the plot level. A total of 20 biotic and abiotic variables (both continuous and categorical) were used as predictor covariates (Supplement 2) and “CHANGE” as a binomial response variable (1 = shift from pure to mixed forests; 0 = no shift from pure to mixed forests). Highly correlated variables ($|r| > 0.8$) were excluded prior to building models (Supplement 3). Then, we computed the full GLM with 16 non-correlated variables and not considering interactions (Supplement 4). Finally, we dropped the variables that were not significant obtaining the reduced model and the deviance percentage explained by the model. Deviance reduction, estimated as: $D2 = (\text{null deviance} - \text{residual deviance}) / \text{null deviance}$, was used as the measure of discrepancy to assess the model goodness-of-fit (Crawley 2013). Statistical assumptions were checked using diagnostic plots of model residuals and by visually inspecting the scatter plot between each predictor and the logit values. Model fitting and pairwise differences were computed with the *R* packages “lme4” (Bates and others 2015) and “emmeans” (Lenth 2016) in the *R* environment (R Core Team 2022). Ultimately, we also analysed the percentage of variance explained by each variable using Hierarchical Partitioning (“hier.part” in *R* environment). This method computes the independent and joint con-

tributions of each variable to a linearized regression by hierarchical decomposition of goodness-of-fit measures of regressions (Log-likelihood) using all subsets of predictors in the data set (MacNally 2002). See Supplementary information for detailed description and results (Supplement 5).

RESULTS

Changes in Iberian Tree Species Dominance and Composition

The analysis of trends for total plots classified as pure and mixed forests from SFI1 to SFI4, accounting for the longest temporal series of SFI in Spain, showed that the number of SFI plots classified as mixed forests increased from 5.9% in 1960 (SFI1) to 23.5% at present (SFI4). This positive trend in the occurrence of mixed forests was confirmed when the SFI4 plots were classified based on the dominance of the juvenile stratum (trees with dbh 2.5 cm–7.5 cm) as a proxy of potential future perspectives (FUT_PERS) (Figure 2a). The increment in mixed forests is confirmed for all forest types, this increment being greater for mixed broadleaved and mixed coniferous and broadleaved forests (Figure 2b). In these two cases, the juvenile stratum in all SFI cycles shows the same trend towards an enlargement of these types of functional groups of forests (Supplement 6). In the case of mixed coniferous forests, the trend of juveniles manifests a potential decrease in the future. In contrast, while broadleaved pure forests remain stable between SFI cycles (Figure 2b) and they could increase in the future (supplement 6), pure coniferous forests show a general gradual reduction between SFI cycles (see Figure 2b and Supplement 6). Associated with these negative trends, we also found a noticeable difference in the juvenile stratum between mixed and monospecific plots, the mean percentages of plots without juvenile stratum in SFI2, SFI3 and SFI4 being 19.6, 17.85, 18.61 and 37.06%, 35.92, 37.14%, respectively, for mixed and pure plots (see detailed results for SFI4 in Figure 3).

Most of the plots displayed no shift in tree-type dominance between SFI cycles (80.1%). However, 19.9% of plots did show changes at plot level (Figure 4a). Most of these changes represent the shift from pure to mixed forest (11.8%), 7.2% have changed from mixed to pure and the rest (0.9%) are pure forests which have undergone a total conversion in composition to other types of pure forest between SFI cycles.

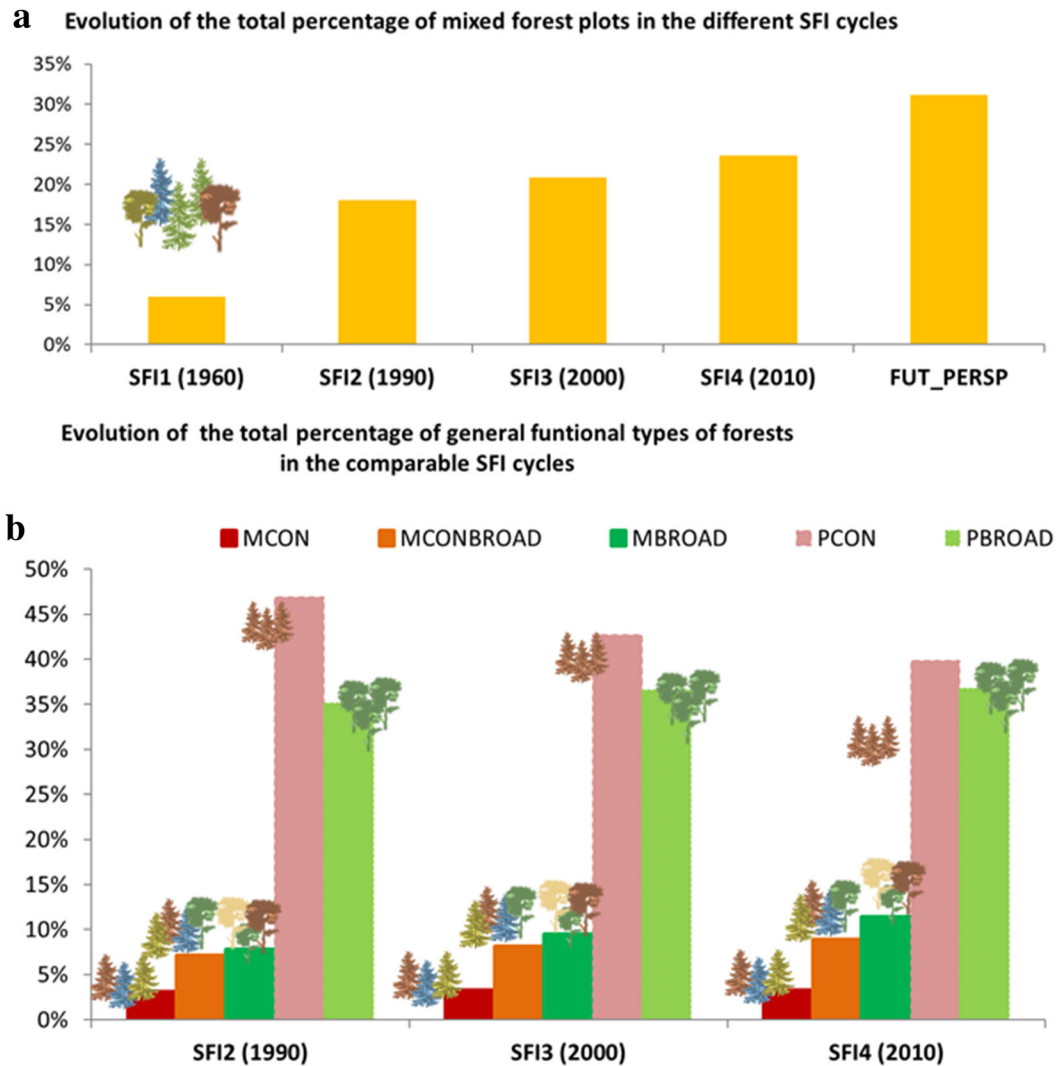


Figure 2. **a** Percentage of plots classified as mixed forest from SFI1 (1960) to SFI4 (2020) at national level. FUT_PERS represents the classification based on the dominance of the juvenile stratum (trees with dbh 2.5 cm–7.5 cm) in SFI4 as a proxy of potential future trends in forest dominance. **b** Evolution of the percentages of plots classified as pure and mixed forests considering general forest types with comparable SFI cycles. MCON: mixed coniferous forests; MCONBROAD: mixed coniferous and broadleaved forests; MBROAD: mixed broadleaved forests; PCON: pure conifer forests; PBROAD: pure broadleaved forests.

By bioregions, the percentages of change in tree dominance and composition between SFI cycles are higher for Atlantic (32.8%) and Alpine (17.2%) forests than for Mediterranean forests (14.8%) (Figure 4b).

The highest percentages of plots with changes per forest type correspond to pure deciduous (21%), followed by pure coniferous (14%), pure marcescents (11%) and pure evergreen forests (10%) (Figure 5). In the case of forests dominated by deciduous, evergreen and marcescent species, most of the changes represent a shift towards mixed

broadleaved forests. However, the changes in forests dominated by coniferous species are more diverse, the most frequent shift being towards mixed forest of conifers with broadleaved evergreen species (Figure 5).

Drivers of Change from Pure to Mixed Forest

The final reduced model for CHANGE (shift from pure to mixed SFI plots) as a response variable included 10 covariates as drivers of the shift from

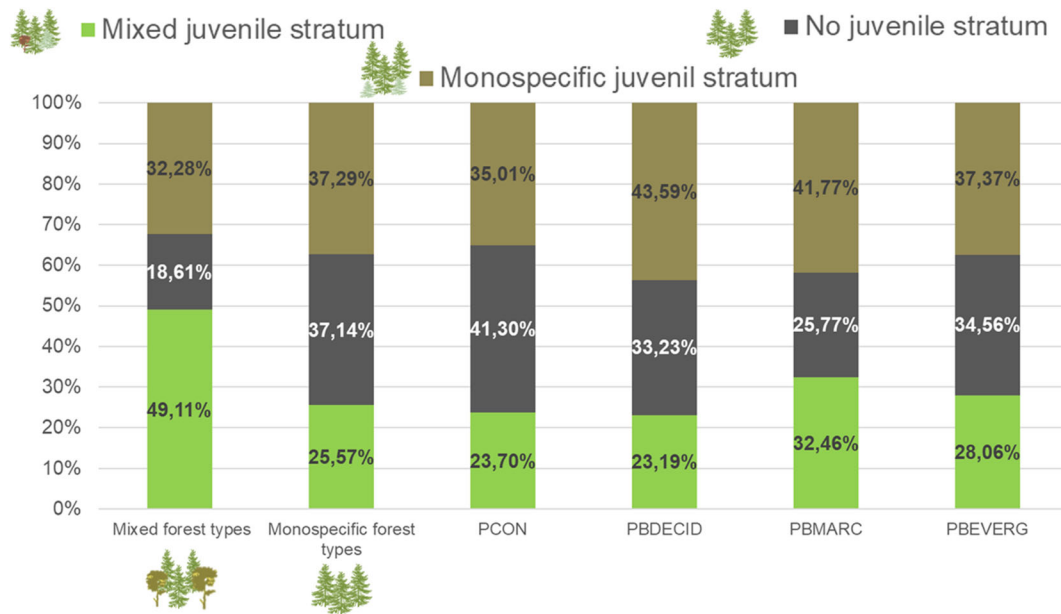


Figure 3. Future perspectives in the dominance of Iberian forests. Percentages of plots of the most recent SFI cycle classified as mixed or monospecific forest types where mixed, monospecific or absent juvenile stratum are shown (trees with dbh 2.5 cm–7.5 cm).

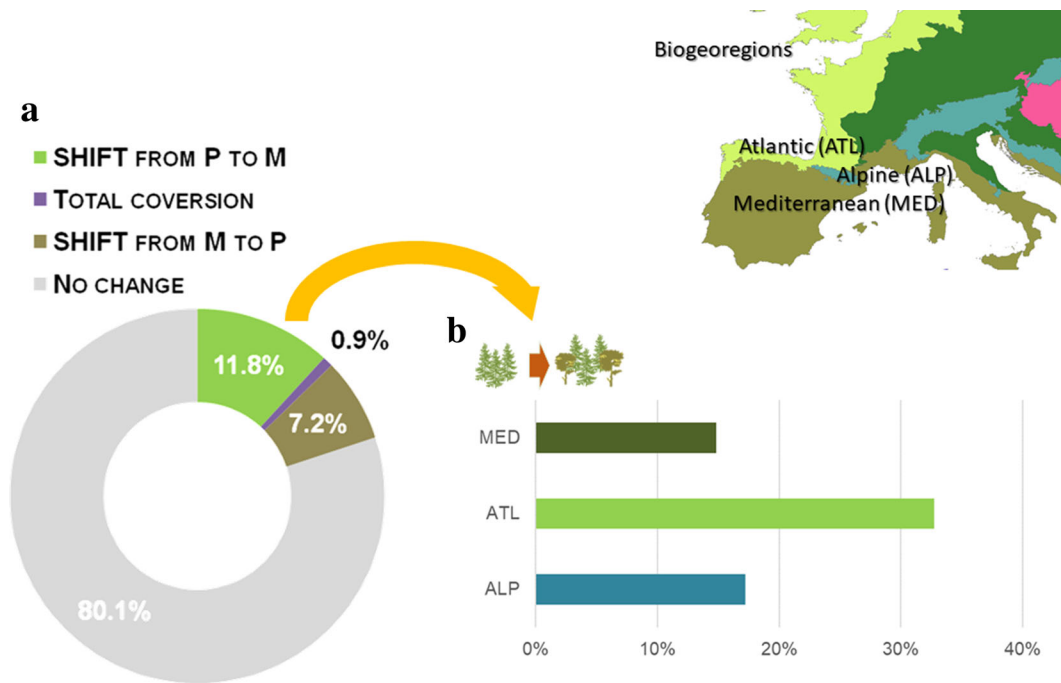


Figure 4. **a** Percentages of the different shifts (P: pure forests, M: mixed forests, total conversion from one P to another P) and no change in dominance registered between continuous SFI cycles in non-intensively managed Iberian Forests. **b** Percentage of SFI plots experiencing shifts from pure to mixed forest between SFI cycles (1986–2020) by biogeoregion.

pure to mixed forest (seven abiotic and three biotic covariates) accounting for 12% of the observed variability (Table 1). Severity of drought and summer precipitation being those factors explain-

ing most of the variance of the selected model (Supplement 5). In addition, the probability of change from pure to mixed forests is greater in areas with greater mean annual temperature as

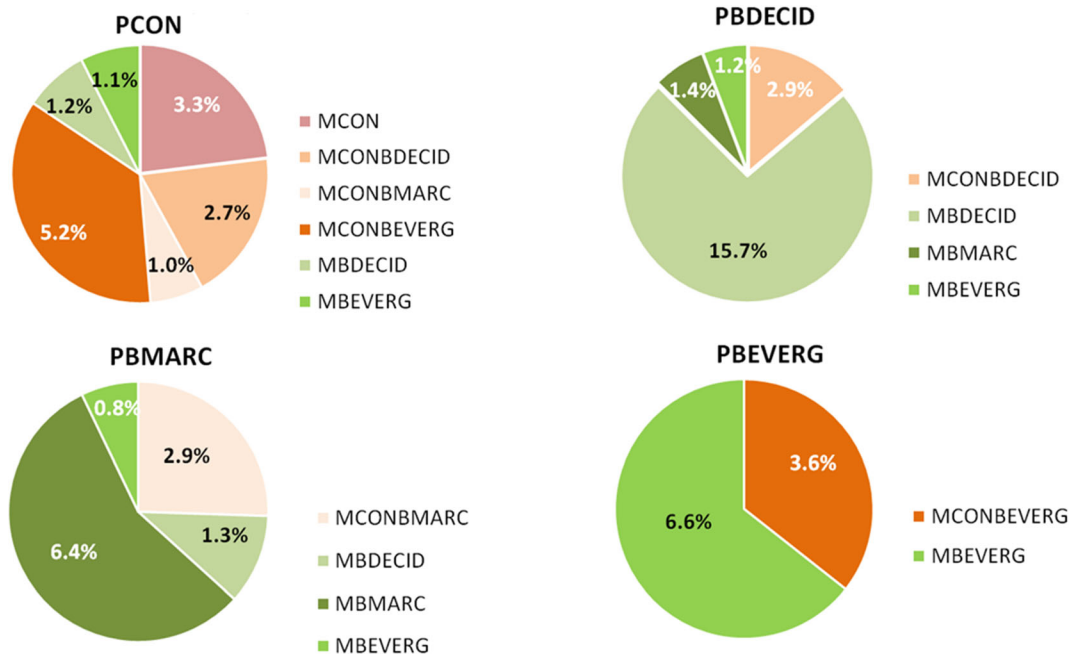


Figure 5. The graphs show the percentage of plots which have shifted from pure to different groups of mixed forests between SFI cycles covering from 1986 to 2020. Monospecific forest types: PCON, conifers; PBEVERG, broadleaved evergreen; PBMARC, broadleaved marcescent; PBDECID, broadleaved deciduous; Mixed forest types: MCON, mixed coniferous forests, MBDECID, mixed broadleaved deciduous forests, MBEVERG, mixed broadleaved evergreen forests, MBMARC, mixed broadleaved marcescent forests, MCONBROAD, mixed coniferous and broadleaved forests.

Table 1. Results of Type II Test of the Reduced Binomial GLM for the Change From Pure to Mixed Forests between SFI cycles

Factors	df	χ^2	P
DCOST	1	(+) 5.044	0.025
PWARMQ	1	(+) 173.494	< 0.001
AMT	1	(+) 88.583	< 0.001
SEV_DROUGHT	1	(+) 4.537	0.033
FOR_TYPE	3	21.527	< 0.001
ALOC	1	(+) 29.461	< 0.001
INALOC	1	(+) 63.297	< 0.001
PROT	1	(-) 4.461	0.035
DIST_SETTL	1	(-) 16.877	< 0.001
CH_POPUL	1	(-) 3.656	0.056

See Supplement 1 for abbreviations of the fixed effects. Data represent the degrees of freedom (df), the χ^2 -statistic with the associated P value of significance (bold type for significant effects, $P < 0.05$). D2 = 11.73. The sign corresponds to the direction of the effect.

well as in areas closer to the coast. This is consistent with previous analyses by bioregions (Figure 4b). In relation to disturbances, the probability of change is greater in SFI plots that have suffered severe drought periods. Concerning biotic factors, change from pure to mixed forests is more likely in broadleaved than in conifer forests (Supplement 7)

and in SFI plots where the presence and increment of non-native tree species over time have been recorded. Finally, with respect to land use variables, the probability of change is greater in those plots located in unpopulated areas with no special protection status but which are close to settlements.

DISCUSSION

From Pure to Mixed Forests

Changes in the dominance of long-lived forest tree species over time are hard to track due to the slow rate of forest ecosystem dynamics and therefore the length of time over which those changes become apparent. Although the results should be interpreted with caution given that the design and objectives of the SFI1 differ from those of the other, comparable, SFI cycles (Alberdi and others 2017); our findings do point to an increase in mixed forests from 1960 to 1986 (12%), more gradual during recent times (from 1986 to 2020, 5.6%), concomitant with a drop in pure conifer forests. Thus, although conversions from mixed to pure stands do come out (7%), they are offset by pure to mixed conversions. This result implies a steady shift in the type of dominance of Iberian forests and also pro-

vides new evidence of the ongoing reorganization of natural communities worldwide (Pecl and others 2017; Seidl and Turner 2022). This positive trend in the occurrence of mixed forests can be observed across all the Iberian biogeographical regions and forest types.

The abovementioned increment in more complex forests is confirmed when we take into consideration the potential future perspectives for forest composition based on the dominance of the juvenile stratum of all continuous SFI cycles. Although this latter proxy should be considered with caution given that stand dominance at these stages of development can easily change and may not represent mature stages (Pretzsch 2009; Heiland and others 2022), the recruitment of trees is a critical process influencing the composition of future forest communities (Carnicer and others 2014). Mixed forests have higher percentages of consistent juvenile stratum (almost 50% with mixed juvenile stratum) compared to pure forests that showed only 37% of their plots with monospecific juvenile stratum. Furthermore, the greater absence of regeneration found in pure forests (36.7% in average, 41% in pure conifers and 31% in average of pure broadleaved SFI plots) compared to mixed forests (18.7%) suggests that this steady, increasing trend towards mixed forests at the expense of pure forests will continue in the future and that mixed forests might constitute stable systems.

In this sense, the generalized failure of regeneration in Iberian forests, more notable in SFI plots dominated by conifer species of *Pinus*, has previously been reported at regional (Urbieta and others 2011) and larger scale (Sheffer 2012; Carnicer and others 2014) studies, highlighting forest succession, climatic limitations, disturbances and management as the main factors affecting the patterns of recruitment in these forests. In this regard, our results also reveal that, in contrast to the dynamic observed in pure broadleaved forests, most of the shifts in dominance from pure conifer forests to mixed forests involve a shift in composition towards mixtures with broadleaved (mostly evergreen) species rather than with other coniferous species. In some cases, a total conversion to broadleaved mixed forest is detected. The increase in tree species richness in coniferous forests caused by the incorporation of broadleaved species is often related to a progressive process of forest succession where old monospecific pine forest plantations are colonized by other tree species, mainly *Quercus* species (Urbieta and others 2011; Sheffer 2012; Carnicer and others 2014; Vayreda and others

2016; Martín-Alcón and others 2015). In the early twentieth century, conifers, mainly pines, were the species most frequently employed in forest restoration and afforestation plans in Spain (Vadell and others 2016). The widespread use of pine was mainly based on the *ecological facilitation concept*, which promoted the large-scale use of monospecific pine plantations given their pioneer behaviour and capacity to adapt to a wide range of environmental conditions, facilitating the subsequent establishment of broadleaved species (Valbuena Carabaña and others 2010). The classical Mediterranean forest succession concept states that these pine-oak mixed forests are transitional stages leading to oak-dominated forests (Capitanio and Carcaillet 2008). However, our results regarding the dominance of the juvenile stratum of pure and mixed forests suggest that mixed forests might become stable alternative successional scenarios. In any case, further research in the future mixed forests stability is still needed.

The significant effect of severe droughts on the shift from pure to mixed plots pointed out by our results may also support the higher stability of mixed forest. Previous works found greater drought resilience in mixed stands compared to pure ones (del Río and others 2017). Thus, the increase in mixed forest in areas affected by severe droughts might be a consequence of the establishment of new tree species combinations better adapted to dry periods. However, again further research is needed because the relationship between drought and admixtures may differ between species, resulting in inconclusive universal pattern (Muñoz-Gálvez and others 2021).

Our modelling also suggests that the greatest prevalence of pure to mixed conversion was observed in temperate zones with higher rates of summer rainfall, that is, the Atlantic biogeoregion, which is the most productive (Vadell and others 2016). In these areas, the effect of the severity of drought is greater since temperate forests are not well adapted to cope with drought events (Anderegg and others 2020; Batlori and others 2020). Furthermore, this area has been influenced by high human population density, intensively managed plantations and small-scale farming practices, many of which are abandoned today (Teixido and others 2010). Accordingly, the shifts in dominance detected were also positively related to land use abandonment and depopulation, confirming the ongoing process of forest re-naturalization and forest recovery towards more complex mixed forests following historical human-induced simplification of Iberian landscapes since the early

Holocene (Carrión and others 2000; Morales-Molino and others 2017).

Furthermore, landscape structure plays an important role in the spread and colonization patterns of invasive plants (Theoharides and Dukes 2007) so current distributions of invasive species frequently reflect historical land use patterns (Pyšek and others 2020). In this regard, we found that the probability of change from pure to mixed forests increases with the presence and increment of non-native species. The Atlantic biogeoregion in northern Spain is reported to be one of the areas with the highest presence and highest risk of invasion of non-native species (Sanz Elorza and others 2003). The combination of favourable climatic conditions, the historical intensive use of the territory and the significant land use changes which have taken place over recent years have promoted the spread and establishment of non-native species. These findings also highlight the important effect of introducing individuals and populations of species beyond their native ranges on the reorganization of natural communities worldwide into emerging novel mixtures and ecosystems (Pecl and others 2017).

Future Perspectives and Implications for Forest Policy and Management

Our results reveal a general increasing trend towards mixed forest in all biogeographical regions, pointing to the recovery of historical more complex forests after centuries of human-induced simplification through land use changes and forest management (Valbuena-Carabaña and others 2010). However, contemporary factors such as climate warming in the form of droughts and the increase in non-native species add more complexity and uncertainty to this natural process of forest recovery by conforming novel or rather hybrid systems of mixed forests. Hence, questions regarding the stability and future perspectives of these enlarging contemporary mixed forests arise: would the composition and structure of some of these new mixed forests remain the same over time? or, are they simply transitional stages, with the ecological succession process leading eventually to the conversion of these forests into other monospecific forests under the current changing climatic conditions? In this regard, there is much debate about whether different mixtures of tree species imply more stable ecosystems since they show more resilience to changes in environmental conditions (Spiecker 2003). Depending on species composition, mixed stands may exhibit niche complementarity as well

as ecological advantages compared to monospecific stands, such as higher productivity, individual growth, and resistance to pests (Cavard and others 2011; Pretzsch and others 2013; Andivia and others 2017). Thus, tree diversity is emerging as an important forest characteristic that enhances forest functions and services and guarantees stability and the capacity to mitigate and adapt to the effects of climate change (but see Sheffer and others 2020; Muñoz-Gálvez and others 2021).

Currently, mixed forests cover approximately 19% of the total Spanish forest area, accounting for 27% in the Mediterranean biogeoregion (Sanchez de Dios and others 2019). Our results indicate that these percentages will increase over the coming decades as a result of the ongoing recovery of forests following historical human-induced simplification together with contemporary climate warming effects. However, the lack of reference definitions and national or international classifications of mixed forest has hampered research on this important type of forests (Bravo-Oviedo and others 2018; Sanchez de Dios and others 2019). The absence of knowledge and basic strategic management tools such as mixed forest classifications could have a negative impact on forest management and conservation of these unexplored forests. On the one hand, our results emphasize the need to continue exploring and researching mixed natural (Waitz and Sheffer 2021) and artificial forests (that is, Bravo-Oviedo and others 2014). On the other hand, regarding the increasing importance of mixed forest identified in this study and their important role in mitigating and adapting to contemporaneous climate change, it is crucial to revise forest classifications as well as forest management and conservation plans in order to include these increasingly abundant contemporary mixed forests.

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DATA AVAILABILITY

We only used public data from the Spanish National Forest Inventory (<https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/default.aspx>).

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