




## RESEARCH ARTICLE

# Recent tree diversity increase in NE Iberian forests following intense management release: A task for animal-dispersed and drought-tolerant species

Miriam Selwyn<sup>1,2</sup>  | Joan Pino<sup>1,2</sup>  | Josep Maria Espelta<sup>1,2</sup> <sup>1</sup>Universitat Autònoma de Barcelona, Bellaterra, Catalonia, Spain<sup>2</sup>CREAF, Bellaterra, Catalonia, Spain**Correspondence**

Miriam Selwyn

Email: [m.selwyn@creaf.uab.cat](mailto:m.selwyn@creaf.uab.cat)**Funding information**

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**Handling Editor:** Akira Mori**Abstract**

1. Under increasing human-related threats to forests, many studies suggest that increasing tree species diversity may boost forest resilience by enhancing the range of species' responses to disturbances. However, it remains unclear whether passive or active forest management strategies should be applied to increase tree diversity. This issue would benefit from investigating which management and environmental factors, together with species' functional traits, influence temporal changes in tree species diversity.
2. We explored the influence of the bioclimatic region, land-use history, forest cover, protection, management, forest structure and changes in temperature and precipitation, to explain tree species diversity changes in NE Iberian forests, by comparing 3141 plots from the Spanish National Forest Inventory sampled between 1989 and 2016. Moreover, we assessed which species' functional traits (dispersal habit, drought and shade tolerance) were most relevant for diversity changes.
3. After 27 years, tree species richness and diversity moderately increased in the tree and regeneration layers. This trend occurred mostly in long-established, non-recently managed forests and in those with a lower initial basal area. Increasing temperature had negative effects for diversity increase in the tree layer but positive for the regeneration compartment, while decreasing precipitation showed the opposite effects.
4. Tree species with higher drought tolerance, and especially those animal-dispersed ones arriving from the regional pool, mostly contributed to the local diversity increase. This pattern occurred in all forest types, although the taxonomic array of species varied.
5. *Synthesis and applications.* The main drivers influencing the passive increase in tree species diversity suggest a primary role of diminishing forest exploitation in this recovery process, fine-tuned by climatic changes. This ecological scenario has particularly favoured animal-dispersed tree species with higher drought tolerance,

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which mostly led the diversity increase. A higher presence of such highly mobile and drought-tolerant species can be crucial to increase functional diversity and, ultimately, increase forest resilience under future scenarios of greater aridity. In light of these results, management strategies should continue fostering the restoration of diversity in once intensively exploited forests while ensuring the maintenance of the already gained tree species diversity.

#### KEYWORDS

drought tolerance, forest diversity, functional diversity, land-use history, life history traits, passive restoration, seed dispersal

## 1 | INTRODUCTION

Natural disturbances are critical drivers of forest composition, structure and functioning (Senf & Seidl, 2021). However, climate change, together with the release of past intensive human land use, may influence the ability of forests to recover after disturbances (Johnstone et al., 2016). Thus, identifying the underpinning mechanisms of forest resilience (i.e. the capacity of forests to absorb disturbances and reorganize after an environmental change, sensu Scheffer, 2020) has become a priority research topic to ensure the maintenance and provision of forest ecosystem functions and services (Johnstone et al., 2016).

Tree species diversity is considered one of the main attributes promoting forest resilience (Jactel et al., 2017; Messier et al., 2022) as it increases the range of tree responses to disturbances (i.e. the insurance hypothesis by Yachi & Loreau, 1999) and provides functional complementarity fostering the efficient use of resources. Thus, numerous studies have emphasized the benefits of promoting tree species diversity by means of either passive natural regeneration or by active tree planting (Haberstroh & Werner, 2022; Messier et al., 2022). Yet, it has also been warned that increasing tree species diversity may require long time periods (Bauhus et al., 2017) and may be constrained by a myriad of factors influencing propagule availability and recruitment, such as changes in the climatic conditions (García-Valdés et al., 2015), land-use legacies (Cruz-Alonso et al., 2021), past and recent management (Chaudhary et al., 2016), forest protection (Lecina-Díaz et al., 2019), and forest structure and cover (Crowther et al., 2015).

Due to the growing interest in the management and environmental factors shaping tree species diversity and the availability of databases resampling the same stands through long periods of time (e.g. National Forest Inventories), an increasing number of studies have examined the trends in tree species diversity through time at regional scales (Crockett et al., 2022; Sánchez de Dios et al., 2023; Vayreda et al., 2013, 2016). Interestingly, although they cover different biogeographic regions, all these studies point out towards an increase in tree species diversity during the last decades of the 20th century onwards, reporting from moderate (Crockett et al., 2022) to rapid shifts (Vayreda et al., 2016), mainly driven by the effects of climate warming and land-use changes. This increase in tree

mixtures (i.e. the 'renaissance' of mixed forests sensu Sánchez de Dios et al., 2023) may have important consequences for forest functioning such as increasing productivity (Bauhus et al., 2017) and resilience to disturbances (e.g. drought stress in Fichtner et al., 2020; forest pests in Blanco-Rodríguez & Espelta, 2022). Nevertheless, the former studies have seldom explored whether such diversity increase arises from local forest dynamics (e.g. ingrowth of seedlings into the tree layer) or from the dispersal and recruitment of species from the regional pool.

In addition to assessing the factors triggering changes in tree species diversity, it will be essential to identify the functional traits of the species involved, as such traits will modulate their ability to surmount the ecological filters shaping recruitment success and, ultimately, the potential complementarity effects in mixed forests. Seed dispersal type has been identified as a primary trait influencing the filtering effects of dispersal, therefore which species, and in what abundance, can be found in an area (Selwyn et al., 2023). Yet, to understand the potential success in tree species recruitment after dispersal, other functional traits influencing environmental filtering such as shade and drought tolerance need to be considered (Thomson et al., 2010). Therefore, different plant functional traits need to be assembled to reveal how dispersal and establishment are linked.

The aims of this study were to analyse forest management and environmental factors influencing temporal changes in tree species richness and diversity in Catalan forests (NE Spain), to explore the role of species functional traits and to assess whether diversity changes were driven by local dynamics at the plot level (i.e. ingrowth and regeneration) or by the arrival of new species from the regional pool. We investigated the role of the bioclimatic region, land-use legacies, forest cover, forest protection, past and recent management, forest structure, and changes in temperature and precipitation over the study period (1989–2016) and considered the changes in both the tree and the regeneration layers, to account for the patterns of tree diversity. Specifically, we addressed three main questions: (i) How have management practices and changes in climatic conditions influenced changes in tree species diversity over time? (ii) Were changes in tree species diversity mostly driven by local dynamics or by the arrival of species from nearby? (iii) Which functional traits (i.e. dispersal method, shade and drought tolerance) have contributed to

changes in forest diversity? The results will help to calibrate the potential extent of passive changes in tree species diversity through time and develop management strategies to maintain and promote tree species diversity and, potentially, enhance forest resilience.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

This research was conducted in Catalonia (NE of the Iberian Peninsula), bounded to the north by the Pyrenees and to the east by the Mediterranean Sea (Figure S1). Forests represent almost 40% of the territory and are characterized by a wide diversity of species and structures, reflecting an outstanding landscape heterogeneity and a long history of forest management (Roces-Díaz et al., 2021). Climate in the region is highly variable—affected by the latitudinal range, a rough topography and the existence of an intense coastal-inland gradient, from warm Mediterranean to temperate-cold climatic regimes. Mean annual temperatures and rainfall range from 18°C and 400mm on the southern coast to 5°C and more than 1500mm in mountain areas (Ninyerola et al., 2000). The most commonly occurring tree species at low altitudes are *Pinus halepensis*, *Quercus ilex* and *Q. faginea*, while *P. sylvestris*, *P. nigra*, *Q. pubescens* and *Fagus sylvatica* dominate at altitudes from 800 to 1500m. Above 1500m, forests are mostly dominated by *P. uncinata* and *Abies alba* (Roces-Díaz et al., 2021).

### 2.2 | Experimental design

#### 2.2.1 | Forest inventory data

To investigate temporal changes in tree species richness and diversity, we used data from the second (NFI2) and fourth (NFI4) Spanish National Forest Inventories, which consist of permanent plots located in a 1 × 1 km grid covering all forested areas of Spain. Our study was based in Catalonia (Figure S1), where the NFI2 and NFI4 took place during 1989–1990 (hereafter 1989) and 2013–2016 (hereafter 2016), respectively (<https://laboratoriforestal.creaf.cat/>). After excluding burnt plots during the studied period (see Figure S1 for details), we obtained 3141 replicated plots systematically sampled in the NFI2 and NFI4 in Catalonia, from which we extracted the species composition and abundance of the tree (individuals ≥ 7.5 cm in dbh) and regeneration (individuals < 7.5 cm in dbh) layers. A total of 71 tree species were recorded in the assembly of the two forest inventories (Table S1).

#### 2.2.2 | Species functional traits

As recruitment success in tree species is shaped by both their dispersal ability and their response to environmental filters

(Cruz-Alonso et al., 2021), we performed a cluster classification according to seed dispersal type: animal-dispersed (dispersed by birds and mammals) versus other dispersal methods, and to shade and drought tolerance. This classification was restricted to the most representative species for which data were available: we excluded tree species recorded in less than five plots (2% of the total number of plots) for both inventories, resulting in a total number of 43 species included for analysis (Tables S1 and S2). Clustering resulted in four distinct groups of species, distinguishing: (C1) animal-dispersed species with lower drought and higher shade tolerance (e.g. *Fagus sylvatica*, *Prunus avium* and *Ilex aquifolium*), (C2) animal-dispersed species with higher drought and lower shade tolerance (e.g. *Crataegus monogyna*, *Arbutus unedo* and *Quercus* spp.), (C3) species with other dispersal methods with lower drought and higher shade tolerance (e.g. *Abies alba*, *Fraxinus excelsior* and *Acer campestre*) and (C4) species with other dispersal methods and higher drought and lower shade tolerance (e.g. *P. nigra*, *P. halepensis* and *Acer monspesulanum*; Figure S2). Notice that although a negative correlation could be expected between shade and drought tolerance, the Pearson correlation test showed a weak negative relationship ( $r = -0.29$ ;  $p < 0.001$ ) and thus, we retained both characteristics for the cluster analysis.

#### 2.2.3 | Factors influencing temporal changes in tree species diversity

##### *Bioclimatic region*

We classified each plot according to the Bioclimatic Classification for Continental Spain, defined by the thermicity index (<https://www.miteco.gob.es>), in order to characterize the long-term climate for each study plot and to identify potential vegetation types of each particular region. We considered three broad bioclimatic regions: (1) mesomediterranean, which is characterized by coniferous, sclerophyllous and mixed forests; (2) supramediterranean, which is characterized by coniferous, semi-deciduous, sclerophyllous and mixed forests; and (3) montane, which is characterized by coniferous and mixed (coniferous-deciduous) forests (Figure S1; Rocés-Díaz et al., 2021).

##### *Land-use history and forest cover*

Land-use history was determined by overlapping the geographical location of each NFI plot with the orthoimages from the American flight B series conducted in Spain in 1956 (<https://www.icgc.cat/>). This allowed for the classification of the NFI plots into two types of land-use history trajectories: (1) 'long existing forests' as those that were already present in 1956 and (2) 'recent forests' as those that were located in pasturelands and croplands in 1956 and established after rural abandonment. The year 1956 is considered a suitable benchmark for distinguishing recent and long-existing forests in the region, because massive expansion of forests occurred during the second half of the 20th century (Cervera et al., 2019). Moreover, previous studies suggest substantial differences in the structure

and functioning of both forest types (Basnou et al., 2016; Espelta et al., 2020). Additionally, the proportion of forest cover surrounding each NFI plot was calculated to account for forest connectivity in the landscape. For such, we used land cover maps derived from Landsat imagery corresponding to the years 1987 and 2017, which reasonably matched our study period (1989–2016) (González-Guerrero & Pons, 2020) and determined forest cover surrounding each NFI plot at 100, 500 and 1000 m. After calculating the Pearson correlation matrix for forest cover at the different distances and years (Figure S3), we selected the proportion of forest cover at 500 m in 1987 as the most accurate measure of connectivity, similar to Basnou et al., 2016.

#### Forest protection

We identified those plots included in the Catalan system of protected areas (<https://sig.gencat.cat/visors/enaturals.html>). This network covers 31% of the territory and includes sites with strict, moderate and partial protection status (one national park, several natural parks, small partial national reserves, national interest sites, provincial parks and other Nature 2000 areas; Lecina-Díaz et al., 2019). For simplicity, we categorized the plots as non-protected versus protected.

#### Past and recent forest management

The occurrence of past forest management (e.g. harvesting), prior to the NFI2, was obtained from evidence (e.g. stumps and woody debris) observed and recorded during the NFI2 field survey in 1989–1990. Additionally, we assessed the occurrence of recent forest management practices between 1986 and 2016 from the disturbance maps developed by Senf and Seidl (2021) using satellite data and manually interpreted reference plots.

#### Forest structure

The basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of the NFI2 plots was also used as a measure of the initial forest structure, as it may potentially influence forest dynamics and habitat suitability for tree establishment (Crowther et al., 2015).

#### Temperature and precipitation changes

We accounted for the effect of recent climate change (i.e. climate variation during the study period) by estimating the absolute change in temperature ( $\Delta T$  [°C]) and the relative precipitation change ( $\Delta P$  [%]) per plot, for the time between inventories. Following a similar approach to that of García-Valdés et al. (2021), we used aggregated data of the years 1988–1992 as representative of the NFI2 period, and the years 2011–2015 as to characterize the NFI4 period, obtained from the Climate Engine database (<https://www.climateengine.org/>) at 9.6 km daily resolution (AgERA5). The trends and summaries of temperature and precipitation changes for the study period are shown in Figure S4. Notice that changes in temperature and precipitation were not correlated ( $r = -0.01$ ,  $p = 0.03$ ) and occurred in all bioclimatic regions.

## 2.3 | Data analysis

### 2.3.1 | Diversity changes between inventories

For each plot and inventory period, we calculated diversity metrics using Hill numbers of order  $q=0$  (i.e. transformation of species richness, hereafter),  $q=1$  (i.e. transformation the Shannon diversity index, hereafter) and  $q=2$  (i.e. transformation of the Simpson diversity index, hereafter; Chao et al., 2010). We also calculated Pielou's evenness index to assess changes among species abundance distributions per plot (Wilsey & Potvin, 2000). For computing the diversity indexes, abundance was established considering the basal area for the tree layer and the count of individuals for the regeneration compartment (Cruz-Alonso et al., 2021). We calculated the absolute change for each diversity metric between NFI2 and NFI4 and conducted Wilcoxon-Mann Whitney tests to determine significant changes. Additionally, we assessed the sensitivity of our results by repeating these analyses using a one-sample *t*-test on log ratios of change (i.e.  $\text{Ln}[\text{DiversityNFI4}/\text{DiversityNFI2}]$ ). We then performed a permutational analysis of variance to test for systematic temporal turnover (i.e. overall directional shifts in composition) between both time periods for the abundance and the presence/absence of tree species composition, for the 3141 plots sampled (see Crockett et al., 2022 for a similar approach).

To analyse whether the bioclimatic region, land-use history, forest cover, protection, past and recent management, forest structure, and temperature and precipitation changes influenced changes in taxonomic diversity for the tree and the regeneration layers, we ran linear models for which the change in each diversity measure was the response variable. We fitted the models scaling continuous variables, without considering interactions given the large number of included explanatory effects, and we chose the best fit by using the Stepwise Algorithm (MASS package, Ciaburro, 2018) and selected the model with the lowest AIC using  $\Delta\text{AIC} > 2$  as an indicator for supporting the more complex model. In addition, we computed the percentage of the variance explained by each variable using the Hierarchical Partitioning method (see Sánchez de Dios et al., 2023 for a similar approach).

### 2.3.2 | Provenance likelihood and functional traits of newly recruited species

By comparing both NFIs, we identified those plots that lost or gained species during the study period. For considering that a plot had lost a species, the species found in the NFI2 should be absent in both the tree and regeneration layers of the NFI4. Because the number of these plots was low (6.3% and 10.7% for the tree and regeneration layers, respectively) in comparison with the number of plots that gained species (39% and 30% for the tree and regeneration layers, respectively), we focused our analyses on those plots that gained species by either changing from monospecific to mixed or from mixed to more mixed stands. For such, we built

a new metric based on the presence/absence information of each species in each plot and NFI period. This metric allowed us to address whether a new species which appeared in the tree or the regeneration layer in NFI4 inventory was already present in the NFI2 and thus recruited from inside the plot (therefore local pool; Figure 1a,c); or the new recruited species was not present in the NFI2 plots and arrived from outside the plot (therefore regional pool; Figure 1b,d).

For the subset of plots exhibiting an increase in species richness, we examined the role of functional traits on the chances of the different species to be recruited from inside or outside the plots. To do so, we carried out generalized linear models for the tree and the regeneration layers in which we analysed the effects of the clustered functional traits and the management and environmental variables reported, on species provenance transformed into a binary variable

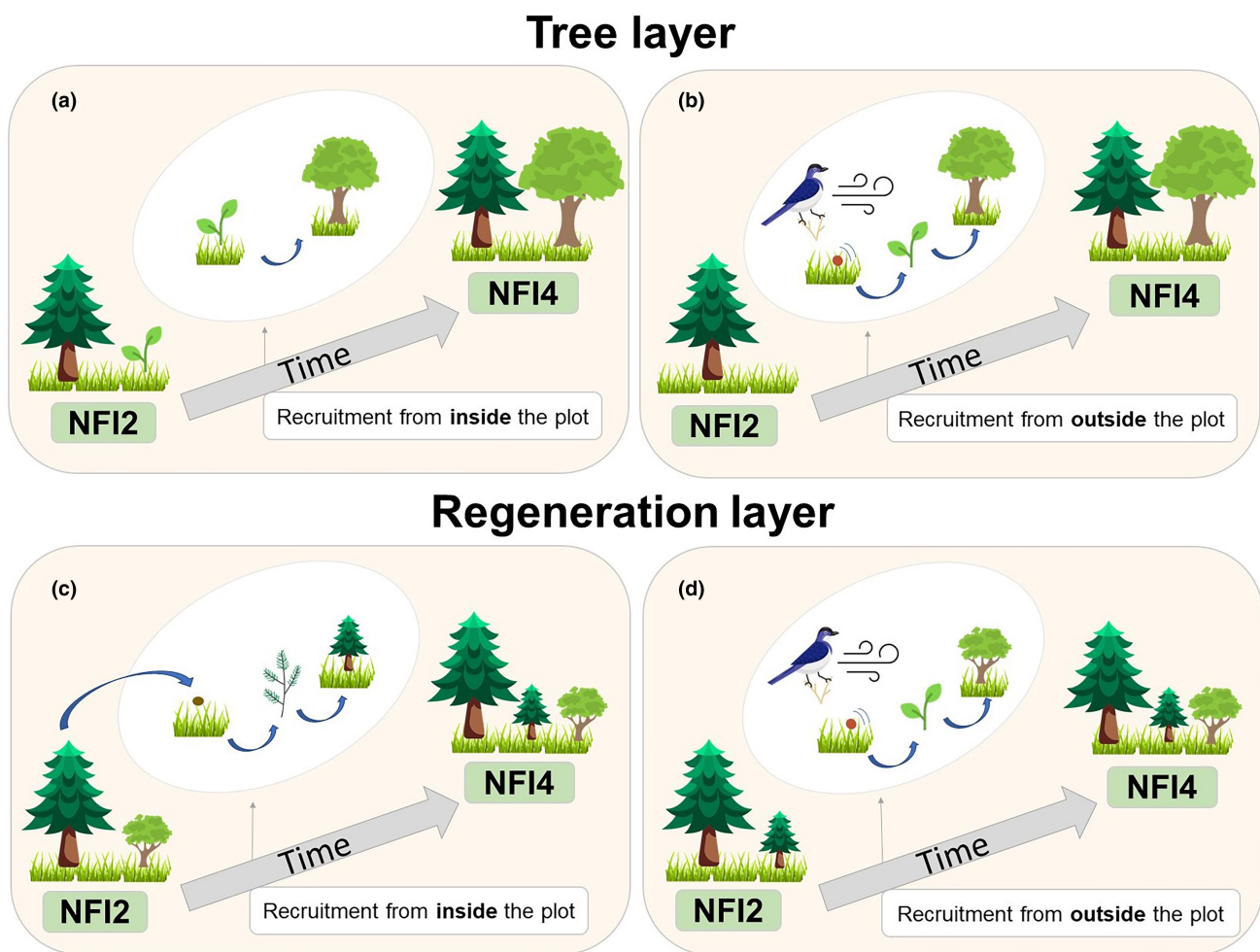
(i.e. inside = 1, outside = 0) and fitted the best model using the same procedure as described above.

All models' residuals were checked for the evidence of spatial autocorrelation and no sign of such was detected for neither the tree nor the regeneration layers (Figures S5 and S6).

### 3 | RESULTS

#### 3.1 | Temporal changes in tree species richness and diversity

The comparison between forest inventories showed a slight but significant increase in tree species richness, Shannon diversity index and Simpson diversity index for both the tree and regeneration



**FIGURE 1** Representation of the origin (local vs. regional pool) of new species recruited in the plots surveyed in the forest inventory in 2016 (NFI4) for the tree (a, b) and regeneration layers (c, d), based on the presence/absence of such species in the previous inventory in 1989 (NFI2). We distinguished four alternative mechanisms for the recruitment of new species: (a) A new species recorded in the tree layer in the NFI4 was considered to be recruited from inside the plot (local pool) as a result of ingrowth if it was already present in the regeneration layer in the NFI2. (b) A new species recorded in the tree layer in the NFI4 was considered to be recruited from outside the plot (regional pool) when it was absent in the regeneration layer in the NFI2. (c) A new species recorded in the regeneration layer in the NFI4 was considered to be recruited from inside the plot (local pool) when it was absent in the regeneration layer but present in the tree layer in the NFI2. This process involved seed production by the local trees and the establishment of seedlings. (d) A new species recorded in the regeneration layer in the NFI4 was considered to be recruited from outside the plot (regional pool) when it was absent in the regeneration and tree layers in the NFI2.



layers (Figure 2), and these results were also confirmed by the sensitivity tests of log ratio changes (Figure S7). Conversely, we did not observe changes in Pielou's evenness index for either the tree or the regeneration layers (Figure 2d,h). The increase in species richness and diversity was also supported by the permutation tests which showed significant compositional change for both the presence/absence and abundance of species for the tree and regeneration layers (Table S3). As a result of the increase in tree species richness for the tree layer, 16% of the plots changed from monospecific to mixed stands, while 23% of the mixed plots became more mixed during the studied period. For the regeneration layer, 21% of the monospecific plots gained species, while 9% of the mixed plots became more diverse. See Figure S8 for the spatial distribution of species richness changes for the tree and the regeneration layers.

The main effects of the linear models explaining diversity change pointed out a significant increase in richness and diversity in the tree layer for the montane and supramediterranean regions compared to the mesomediterranean one, while for the regeneration layer, an increased pattern was observed in all bioclimatic regions (Tables S4–S9; Figure 3). Also, changes in temperature and precipitation during the study period showed contrasting effects for the tree and regeneration layers: that is, while for the tree layer, increasing temperature coupled with a lower decrease in precipitation negatively affected the increase in richness and diversity (Figure 3a–c), it had positive effects for the regeneration layer (Figure 3d–f). In addition to the influence of environmental effects, three variables related to forest management showed similar effects for the two compartments: that is, the increase in species richness and diversity was higher in long-established forest plots while recent management and a higher total

basal area showed a negative effect (Figure 3). In addition, for the regeneration layer, past management did also negatively influence diversity (Figure 3e) while forest protection showed a positive effect (Figure 3d,e). For all models, the total percentage of the variance explained was less than 10% (Tables S4–S9), even so, the percentage of the variance explained by each variable's effect was significant in light of the results of the Hierarchical Partitioning analysis (Figure S9).

### 3.2 | Provenance likelihood and functional traits of newly recruited species

As shown in Figure 4, for the subset of plots that experienced an increase in tree species richness, most recruitment events of new species corresponded to species with higher drought tolerance both in the tree and the regeneration layers (ca. 75% and 65% of events, respectively), primarily dispersed by animals (Cluster 2; ca. 60% and 50%, respectively) and secondarily by other methods (Cluster 4; ca. 20% for both the tree and regeneration layers).

Recruitment of new species in any of the two layers occurred from inside and outside the plots but differences were observed for the tree and the regeneration layer depending on the functional traits and some of the forest and environmental characteristics (Tables S10 and S11). For the tree layer, recruitment of animal-dispersed species with higher drought (i.e. Cluster 2) significantly corresponded to individuals arriving from outside the plots (Figure 5a). Regarding environmental and management characteristics, higher values of forest cover surrounding the plots prompted the arrival and recruitment of these new species from outside the plots (Table S10). While we did

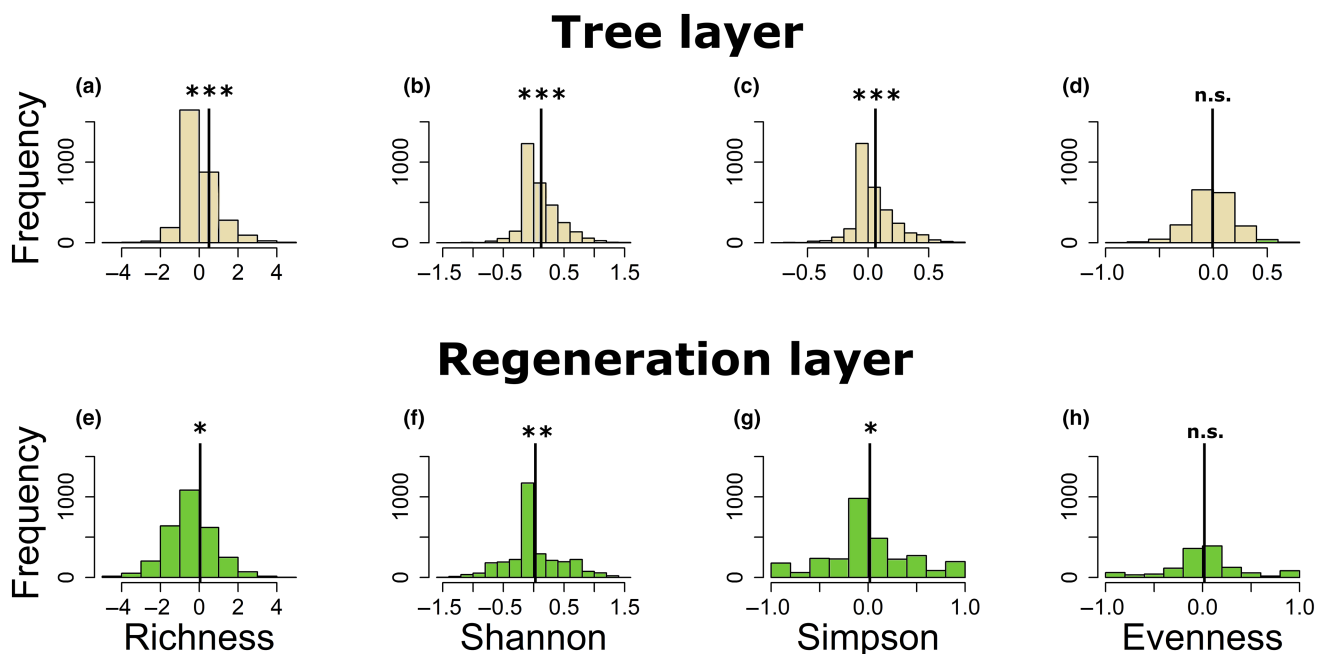
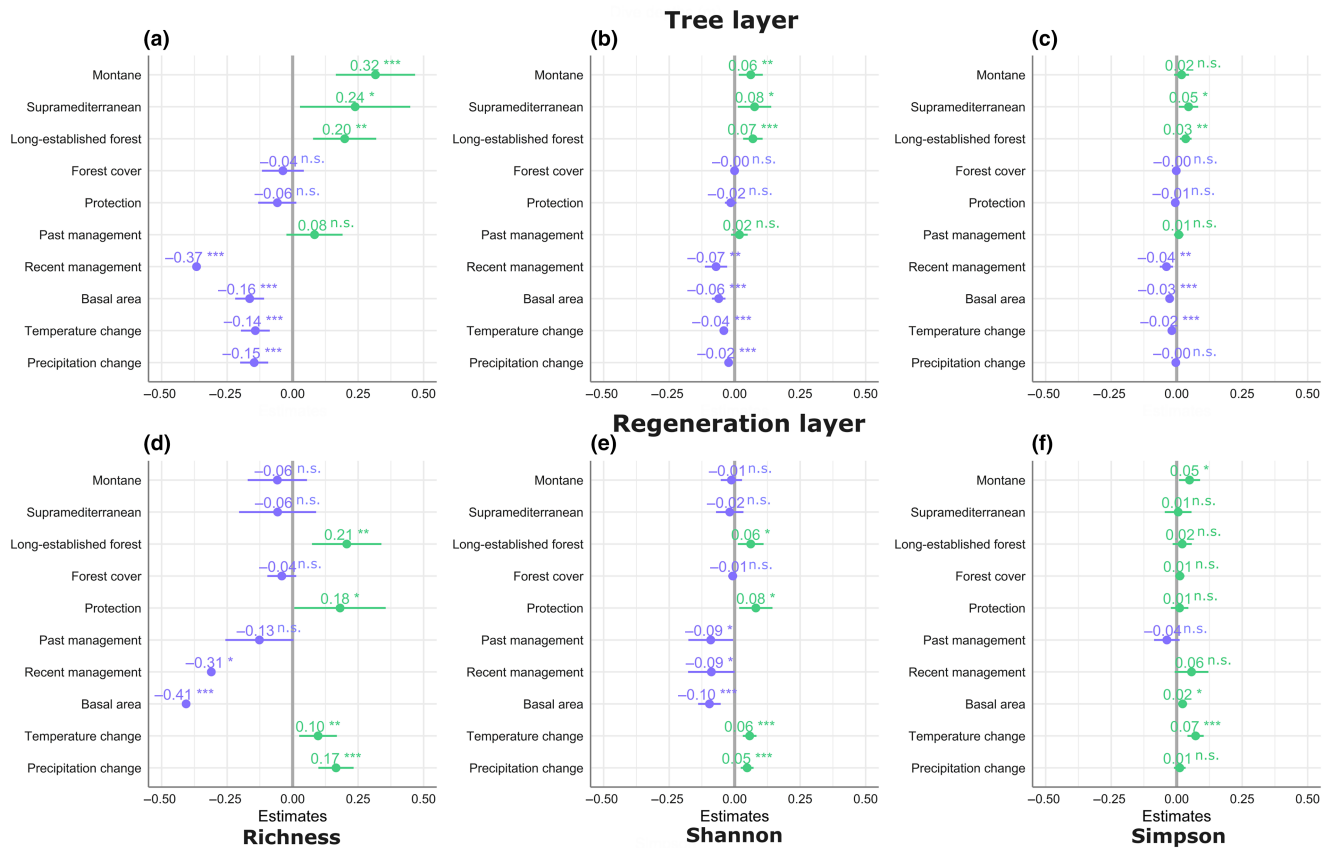


FIGURE 2 Mean change (black bar) from 1989 to 2016 for tree species richness, Shannon diversity index, Simpson diversity index and Pielou's evenness index for the tree (a–d) and the regeneration layers (e–h) for plots of the Spanish National Forest Inventory in Catalonia (NE Spain). Asterisks indicate significant differences according to the Wilcoxon–Mann–Whitney paired tests (\* = 0.05; \*\* = 0.01; \*\*\* = 0.001; n.s. = non-significant).  $N = 3141$  plots.



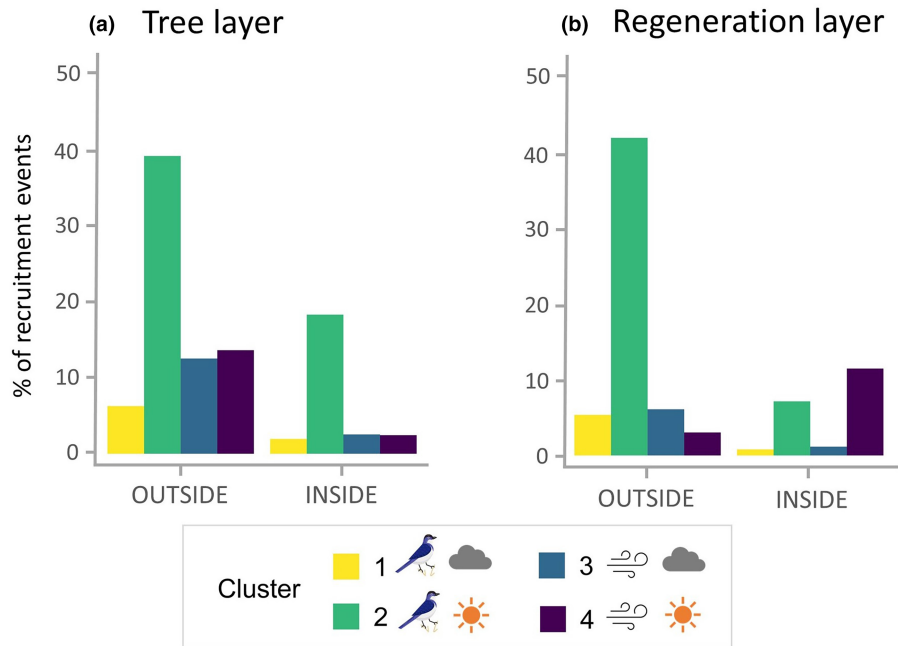
**FIGURE 3** Parameter estimates for the linear models explaining the effects of forest management and environmental variables in the changes in tree species richness, Shannon diversity index and Simpson diversity index from 1989 to 2016 in the National Forest Inventory plots, for the tree (a–c) and the regeneration (d–f) layers. The explicative variables include the bioclimatic region, land-use history, forest cover, protection, past and recent management, basal area, and temperature and precipitation changes. Estimates, confidence intervals and  $p$ -values can be found in Tables S4–S9. Asterisks indicate the significance of each effect (\* = 0.05; \*\* = 0.01; \*\*\* = 0.001; n.s. = non-significant).

not observe any significant effects of the bioclimatic region, protection, recent management, basal area or changes in temperature and precipitation. For the regeneration layer, the prevalence in the recruitment of new species arriving from outside the plot only occurred in the montane bioclimatic region (Table S11). In this layer, the preferential recruitment of animal-dispersed species with higher drought tolerance (i.e. Cluster 2) from outside the plots was only marginally significant (Table S11; Figure 5b), while species with similar levels of drought tolerance but non-animal dispersed (i.e. Cluster 4) were significantly recruited from inside the plots (Table S11; Figure 5b). Similar to the observations for the tree layer, no effects of differences in land-use history, forest protection and structure and changes on temperature and precipitation were observed. The performance measurement of the generalized linear model for the tree layer was slightly lower than that for the regeneration layer, but both showed good classification fit values (ROC-AUC > 0.60, Tables S10 and S11).

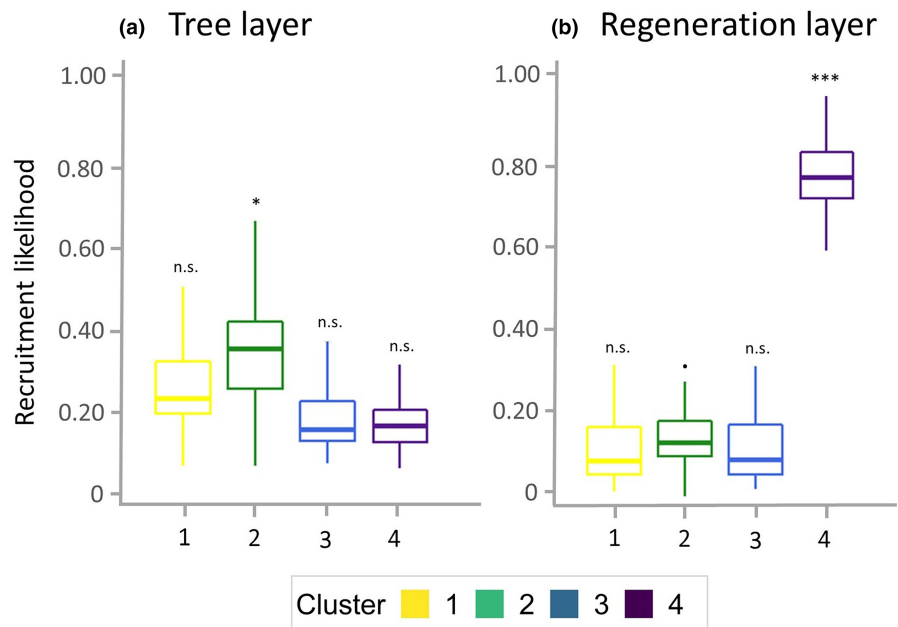
## 4 | DISCUSSION

Increasing tree species diversity to adapt forests to climate change and human-related disturbances is a primary objective claimed by the

scientific community (Messier et al., 2022) that is also gaining momentum in the political agendas (e.g. the European Union's Biodiversity Strategy for 2030). Yet, the time required to achieve this diversity increase as well as which strategies (i.e. active or passive) should be applied are still under debate. Overall, the passive increase in tree species diversity reported here is in line not only with the signs of recovery of mixed forests reported in other studies varying in their spatial and temporal scale (Sánchez de Dios et al., 2023; Vayreda et al., 2013, 2016 for the Iberian Peninsula) but also in other biomes (e.g. Crockett et al., 2022 for northern forests), a pattern that has been attributed to both climate and forest management changes. In our region, the fact that the higher increase in tree species diversity occurred mostly in long-established, non-recently managed forests and those that initially exhibited lower values of basal area (Tables S4–S9; Figure 3) reflects a trend towards the recovery of tree diversity, after a well-known history of extensive land-use changes and intense forest management that resulted in the impoverishment of tree diversity and the homogenization of forest composition (Cervera et al., 2019; Sánchez de Dios et al., 2023). Yet, our results highlight that after the release from intensive management, changes in tree diversity are also being fine-tuned by climatic (i.e. temperature and precipitation) trends (Cruz-Alonso et al., 2021; Rocas-Díaz et al., 2021). Notwithstanding



**FIGURE 4** Recruitment events (%) of tree species from inside or outside the plots for the tree (a) and regeneration (b) layers for the subset of plots where tree species richness increased. Species were classified according to their dispersal mode (animal vs. other methods) and drought and shade tolerance (Figure S2). Clusters: 1 (yellow)=animal-dispersed species with lower drought and higher shade tolerance; 2 (green)=animal-dispersed species with higher drought and lower shade tolerance; 3 (blue)=species with other dispersal methods with lower drought and higher shade tolerance; and 4 (purple)=species with other dispersal methods and higher drought and lower shade tolerance. Note that the number of recruitment events differs for the tree and regeneration layers as a different number of plots gained species during the study period.



**FIGURE 5** Recruitment likelihood probability from inside (i.e. 1) or outside (i.e. 0) the plots for species with different functional trait characteristics (i.e. cluster category) for the tree (a) and the regeneration (b) layers. Asterisks indicate the significance of differences in origin (i.e. inside vs. outside) of recruitment ( $\cdot = 0.1$ ;  $* = 0.05$ ;  $*** = 0.001$ ; n.s. = non-significant). See Figure 4 for cluster codes.

this, we must acknowledge the low explanatory power of our models, in line with other studies that evaluated temporal changes in tree species diversity at local scales ( $\alpha$ -diversity; e.g.  $R^2 < 20\%$  in Basnou et al., 2016;  $R^2 < 15\%$  in Cruz-Alonso et al., 2021;  $R^2 < 5\%$  in

García-Valdés et al., 2021). This suggests the relevance that stochastic community processes (Crockett et al., 2022) or filters imposed by past disturbances events (Espelta et al., 2020) may have in shaping tree species diversity at small spatial scales, in comparison with more



evident changes at the landscape level (Crockett et al., 2022; Cruz-Alonso et al., 2021; Espelta et al., 2020). In addition, the fact that the moderate diversity increase was mostly driven by changes in species richness, rather than by changes in evenness (i.e. no differences in the Pielou index, Figure 2), suggests that the period analysed (ca. 30 years) may still be too short to detect relevant effects of forest management and environmental changes in the dominance of particular tree species.

Non-environmental factors influencing overall changes in tree species diversity showed similar effects for the tree and the regeneration layers: that is, the increase in species richness and diversity was higher in long-existing forests than in recently established ones, and it was negatively affected by recent management and by higher values of basal area in the forest (Tables S4–S9; Figure 3). Considering that long and recently established forests in the area currently exhibit similar tree species richness and diversity (Basnou et al., 2016; Cruz-Alonso et al., 2021), the reported effect of land-use age on increasing forest diversity showcases a process of tree species recovery in long-existing forests where intensive past management and other disturbances had eroded their original tree diversity (Espelta et al., 2020). In addition to forest land-use age, our results revealed a self-evident negative effect of recent forest management for the increase in tree species diversity. These negative effects could be caused, for the tree layer, by the deliberate biased harvesting of particular tree species, as well as the negative effects of harvesting methods for the regeneration compartment (e.g. trampling, selective elimination of some particular tree species). Finally, the observed negative influence of an initial high basal area for tree diversity increase (Tables S4–S9; Figure 3) could stem from two different effects. First, it may result that intense competition among trees in more developed stands determines scarce opportunities for the recruitment of new tree species (Vayreda et al., 2016). Second, we cannot discard that some forests with high basal area values correspond to mature forests where tree species richness has already reached, or approached, maximum levels (i.e. most, if not all, species present in the regional pool are already represented), and therefore further increases are unlikely to occur (Hilmers et al., 2018).

In addition to the paramount effects of factors related with land-use history and forest management, our study pinpointed a greater tree diversity increase for the tree layer in the supramediterranean and montane bioclimatic regions, which could be partially explained by the fact that the decrease in anthropogenic activities (i.e. forest exploitation and livestock grazing) occurred earlier and to a greater extent in mountain areas (Peñuelas et al., 2017). Moreover, differences in temperature and particularly in precipitation between the two inventories also affected the possibility of tree species diversity increase with contrasting importance and results for the tree and the regeneration layers: that is, for the tree layer increase in diversity was lower in forests that experienced higher warming or a lower decrease in precipitation while the reverse situation was observed for the regeneration compartment (Tables S4–S9; Figure 3). The patterns observed for tree layer could be related with the observed higher occurrence and impact of tree decay and mortality episodes in areas that are becoming warmer

but relatively stable in precipitation and are occupied by species at their southernmost distribution limit (e.g. *Pinus sylvestris*, *Fagus sylvatica*), more sensitive to increasing drought events than Mediterranean drought-adapted species (Chaparro et al., 2016). In contrast, the positive effects observed for the same climatic trends for the regeneration layer could stem from the opportunities for seedling recruitment appearing in those forests that are experiencing tree decay and mortality episodes (see for recruitment opportunities related to drought effects: Espelta et al., 2011). Nevertheless, temperature and precipitation changes had lower relevance in comparison with forest management effects (i.e. basal area) in driving changes in tree species diversity (Figure 3; Figure S9). This pattern was also observed by other studies investigating temporal changes in the provision of ecosystem services in the same study area (Roces-Díaz et al., 2021) and highlights that climate change effects are not yet the main drivers of forests dynamics compared to the release in forest management.

The more relevant species contributing to the observed increase in tree diversity were those with higher drought and lower shade tolerance habit (i.e. Clusters 2 and 4 in Figure 4) and, particularly by those animal-dispersed species (i.e. Cluster 2 in Figure 4). The advantages of relatively high drought tolerance traits are consistent with the characteristics of the forests experiencing higher diversity increase: that is, (open) forests with lower initial basal area (Figure 3). In addition, the combination of these ecophysiological traits with animal seed dispersal may be especially appropriate to surmount the dispersal and environmental filters constraining tree recruitment in forest landscapes secularly affected by intense exploitation and habitat fragmentation in a climate characterized by water stress. In this scenario, seeds of animal-dispersed species can reach longer distances than those dispersed by other methods resulting often in an overrepresentation of the former species in highly isolated patches (Basnou et al., 2016). In addition, the directional dispersal of seeds towards suitable microsites (e.g. under shrubs) by the seed dispersers involved (e.g. *Garrulus glandarius*, *Pica pica*, *Turdus* spp. and *Apodemus sylvaticus* in the region) and their catching behaviour (e.g. protecting seeds under litterfall) may facilitate the successful establishment and growth, especially in a climate (i.e. Mediterranean climate) with chronic water stress (Martínez-Baroja et al., 2019; Zavala et al., 2011). Interestingly, the genus *Quercus* dominates the cluster of animal-dispersed species with higher drought tolerance chiefly contributing to forest diversity (Figure S10A), a result that is in line with the recently reported expansion of oaks in Spanish forests (Sánchez de Dios et al., 2023; Vayreda et al., 2016). Yet, despite this relevance, it is important to highlight that other species and genus from the same cluster (e.g. *Sorbus* spp., *C. monogyna*, *Phillyrea latifolia* and *A. unedo* in Figure S10A) are also contributing to forest diversity increase. Thus, the key role of animal-dispersed species with higher drought tolerance for tree diversity increase appears replicated in all bioclimatic regions, although involving different taxonomic identities: for example, *A. unedo* in mesomediterranean pine forests while *C. monogyna* in montane ones (Figure S10A). In all cases, higher forest cover appears to be a relevant factor driving the likelihood of recruitment of these species from the regional pool (Table S10), in line with the general

benefits of connectivity among forest patches for seed dispersal by animals emphasized in previous studies (Selwyn et al., 2023).

Although the increase in species diversity was driven by the incorporation of new species either in the tree or in the regeneration layer from both the local and regional pools (i.e. inside or outside the plots), our analyses revealed differences for the two compartments (Figure 5). For the tree layer, the pre-eminent contribution of animal-dispersed species arriving from outside the plots is consistent with a massive early arrival of seeds of these species and their growth in monospecific conifer forests (Figure S11A, see also Gómez, 2003). This process would reflect the classical Mediterranean forest succession path of pine-oak forests as a transitional stage leading to oak-dominated forests (Zavala et al., 2011). For the regeneration layer, the advanced contribution of species with higher drought and lower shade tolerance but non-animal-dispersed (Figure S10B) mostly corresponded to conifers recruited in plots dominated by broadleaved species in the NFI2 (Figure S11B). Such contribution of conifers to increase the diversity of the regeneration layer could be related to recent extreme drought events and other forest decay episodes that severely affected broadleaved species (Chaparro et al., 2016). In contrast with the more classical successional theories, this situation would highlight that mixed conifer-broadleaved forests could increasingly become a stable alternative successional scenario under the current effects of climate change (Sánchez de Dios et al., 2023).

Ultimately, the higher recruitment of drought-tolerant species reported in our study could be crucial to enhance the resilience of NE Iberian forests under an aridity increase derived from climate change (García-Valdés et al., 2021). On the one hand, this benefit would be achieved per se by the benefits of the particular functional traits of these newly recruited species to surmount water shortage. In addition, resilience in more diverse forests can also be promoted by the facilitative effects of higher levels of resource partitioning (e.g. soil water) among different neighbours (Fichtner et al., 2020; Grossiord, 2019; Pretzsch et al., 2013) or other effects such as microclimate partitioning or biotic facilitation. In this line, future research should be aimed to gain a more precise knowledge of the functional complementarity existing among the different species involved in the recent assembly of the mixed forests reported in this study.

## 5 | CONCLUSIONS

For the last ca. 27 years, tree species richness and diversity has slightly increased in NE Iberian forests, influenced mostly by land-use history, a release in the intensity of exploitation and changes in temperature and precipitation trends. Regarding forest characteristics, the fact that diversity increase was higher in long-existing forests highlights the need to foster the restoration of diversity in those secularly disturbed forests. In this line, shifting the exploitation towards more recently established and highly productive forests (Frei et al., 2023) could be considered to encourage this restoration process. In addition, the negative consequences of recent forest management for tree species diversity also stresses the need to promote

silvicultural practices tailored towards biodiversity conservation (e.g. close to nature forestry). This scenario could benefit the establishment of animal-dispersed tree species, which in combination with a higher drought tolerance are the ones leading the increase in tree species diversity. Ultimately, a higher presence of such highly mobile species may promote forests' 'insurance capacity' (Messier et al., 2022) by enhancing their ability to resist droughts and, potentially, other human threats.

## AUTHOR CONTRIBUTIONS

Miriam Selwyn, Joan Pino and Josep M. Espelta conceived and designed the research and contributed to the final edition of the manuscript; Miriam Selwyn performed the data acquisition and analysis and wrote the manuscript with the advice of Josep M. Espelta.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.q83bk3jqg> (Selwyn et al., 2024).

## ORCID

Miriam Selwyn  <https://orcid.org/0000-0002-3773-1734>

Joan Pino  <https://orcid.org/0000-0003-0939-7502>

Josep Maria Espelta  <https://orcid.org/0000-0002-0242-4988>

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1:** Study area and geographical distribution of the National Forest Inventory plots considered in our study of Catalonia (NE Spain).

**Figure S2:** Dendrogram of the hierarchical cluster classification for each tree species in relation to their dispersal method, shade tolerance and drought tolerance functional trait data.

**Figure S3:** Pearson correlation matrix for the proportion of forest cover (%) surrounding the NFI plots at 100, 500 and 1000m radius derived from land cover maps of Catalonia for the years 1987 and 2017.

**Figure S4:** Trends and summaries of temperature (A) and precipitation (B) changes during 1988–1992 (as representative of the NFI2 period), and the years 2011–2015 (as representative of the NFI4 period).

**Figure S5:** Results of the residual's spatial autocorrelation test for the linear mixed effect models explaining species richness change, Shannon diversity index change and Simpson diversity index change for the tree and regeneration layers.

**Figure S6:** Results of the residual's spatial autocorrelation test for the generalized linear mixed effect models explaining recruitment likelihood from inside (i.e., 1) or outside (i.e., 0) the plots for the tree (A) and regeneration (B) layers.

**Figure S7:** Tree and regeneration layer's sensitivity tests of log ratio changes for species richness (Hill number  $q=0$ ), Shannon diversity index (Hill number  $q=1$ ) and Simpson diversity index (Hill number  $q=2$ ).

**Figure S8:** Spatial distribution of species richness changes for the plots of the Spanish National Inventory in the study area during the study period (1989–2016) for (A) the tree layer, and (B) the regeneration layer.

**Figure S9:** The percentage of variance explained by each variable using the Hierarchical Partitioning method, which shows the goodness of Fit Calculation by randomizing each explicative variable.

**Figure S10:** Distribution of those newly recruited species according to the three bioclimatic regions studied for (A) the tree layer and those animal-dispersed, higher drought and lower shade tolerant species (Cluster 2), and (B) the regeneration layer and those species dispersed by other methods, higher drought and lower shade tolerant (Cluster 4).

**Figure S11:** Species assemblage in the NFI4 plots (2016) resulting from the sum of the incorporation of new species (green bars) recruited together with those species already present in the NFI2 (1989) inventory (black bars).

**Table S1:** List of tree species ( $N=71$ ) present in the national forest inventory (NFI) dataset for Catalonia.

**Table S2:** Tree species functional trait data regarding seed dispersal type, shade tolerance and drought tolerance, together with each species cluster classification according to the three studied functional traits.

**Table S3:** Permutation test results for the tree and regeneration layers' tree species abundance and presence/absence data.

**Table S4:** Results of the linear model for species richness change from the NFI2 (1989) to the NFI4 (2016) for the tree layer.

**Table S5:** Results of the linear model for the Shannon diversity index change from the NFI2 (1989) to the NFI4 (2016) for the tree layer.

**Table S6:** Results of the linear model for the Simpson diversity index change from the NFI2 (1989) to the NFI4 (2016) for the tree layer.

**Table S7:** Results of the linear model for species richness change from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer.

**Table S8:** Results of the linear model for the Shannon diversity index change from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer.

**Table S9:** Results of the linear model for the Simpson diversity index change from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer.

**Table S10:** Results of the generalized linear effect model explaining recruitment likelihood from inside (i.e., 1) or outside (i.e., 0) the plots and the role of species functional traits for recruitment from the NFI2 (1989) to the NFI4 (2016) for the tree layer.

**Table S11:** Results of the generalized linear effect model explaining recruitment likelihood from inside (i.e., 1) or outside (i.e., 0) the plots and the role of species functional traits for recruitment from the NFI2 (1989) to the NFI4 (2016) for the regeneration layer.

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