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Nested plot designs used in forest inventory do not accurately capture tree species richness in Southwestern European forests

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Abstract

Key message Nested plot designs with concentric plots with increasing radii and size threshold underestimate tree species richness with respect to full census sampling with no tree size restrictions. Regeneration emerged as the most relevant pool for tree species richness estimation.

Context Nested or concentric plot designs, where trees are sampled according to their size and position, are common in National Forest Inventories (NFI) to reduce the sampling effort. However, this could bias the estimation of tree diversity such as species richness.

Aims The main goal of this study is to quantify the effect of the nested plot designs with increasing radii and diameter at breast height threshold on the number of tree species as well as to provide values for mean tree species richness per plot at the forest-type level using the Spanish NFI.

Methods We compared tree species richness according to the Spanish NFI nested plot design (radii ranging from 5 to 25 m with increasing minimum threshold in dbh from 7.5 to 42.5 cm as well as the regeneration compartment) with the richness estimate based on a full census (without restrictions in the location or size) in the Spanish NFI 25 m radius plot.

Results Our results confirmed the underestimation of tree species richness (around 32.5%) when using the nested design. The species omitted in the nested design sampling are often subordinates, typically with small diameters. Regeneration emerged as the main pool for tree species richness estimation. This pattern holds across the main forest types, indicating that it is a generalized rather than regional or local phenomenon.

Conclusion We strongly recommend using full census data for assessing tree species richness whenever available, as relying solely on nested designs can significantly underestimate tree species richness.

Keywords Big data, Biodiversity monitoring, Ecosystem functionality, Forest communities, Mediterranean, Sampling, Species composition, Woodlands

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1 Introduction

Tree species richness is a crucial measure of biodiversity in forest ecosystems (Portier et al. 2022). It holds particular significance as numerous studies have indicated that forests with a greater diversity of tree species tend to be more resilient to both biotic and abiotic disturbances (Pardos et al. 2021). Moreover, diverse forests, characterized by multiple tree species, are more productive than



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less diverse forests (Liang et al. 2016; Zeller et al. 2018), although the extent of these relationships appears to be influenced by the specific forest type (Vilà et al. 2007; Bravo-Oviedo et al. 2021).

There are several approaches to estimating tree species richness depending on the scale of measurement (from sampling point to landscape scale), sampling area, or sampling effort. At the sampling point scale, tree species richness is referred to as the number of tree species in a given area (Chao and Chiu 2016), a proxy of α -diversity. At landscape scale, tree species richness is usually calculated as the total number of tree species in the landscape, a proxy of γ -diversity (Whittaker 1960). However, the number of tree species may underestimate diversity measures since the true number of species is unknown (Chiarucci 2012). Furthermore, as the sampling area increases, the number of species also increases. This relationship is known as the specific-area relationship (Arrhenius 1921; Condit et al. 1996). This relationship, however, might be asymptotic. Therefore, approaches to correct this bias are required (Walther and Morand 1998; Xu et al. 2012; Chao and Chiu 2016; Portier et al. 2022).

National Forest Inventories (NFIs) play a crucial role in forest biodiversity monitoring at large spatial scales (Chirici et al. 2011). They are representative of the entire forest area of the countries and include periodic remeasurement, allowing for spatiotemporal assessments (Moreno-Fernández et al. 2016). NFIs must report a wide number of forest variables for international information requirements and become multi-objective inventories (Alberdi et al. 2017). NFIs are one of the most important sources of information for estimating tree diversity indicators in forests (Chirici et al. 2012). Species richness in NFIs is frequently estimated as the number of tree species assessed in the plot area corresponding to the "Indicator 4.1. Tree species composition of Forest Europe" (Chirici et al. 2012; Forest-Europe 2015; Traub and Wüest 2020). Tree species richness derived from NFIs has been widely used in various applications, such as monitoring forest diversity at different scales (Ghadban et al. 2021; Bravo-Oviedo et al. 2021) or as a predictor in modelling approaches (Ruiz-Benito et al. 2012). However, the heterogeneity of NFI designs poses challenges for comparing tree species richness (Portier et al. 2022) and even for estimating tree species richness within a single country (Lin et al. 2020). This is the case with countries using nested or concentric plot designs (see France, Japan, Russia, Spain, and Switzerland, among others). In this type of plot design, the trees are sampled according to their distance to the plot center as well as to a tree variable (commonly the tree diameter) to reduce the sampling effort for smaller trees in favor of larger trees, which contribute a greater share to total volume (Kershaw et al. 2016; Vidal et al. 2016). Therefore, not every tree within the nested plot is sampled, which can underestimate the tree species with respect to census without restrictions of tree size or location, due to the combined effect of size threshold and concentric plots radii (Arrhenius 1921; Lin et al. 2020; Portier et al. 2022). The concentric plot radius is tightly linked to the specific-area relationship, which states that larger areas contain larger number of species (Arrhenius 1921; Condit et al. 1996). This relationship, however, is curvilinear and may have an asymptote (Walther and Morand 1998; Chao and Chiu 2016; Portier et al. 2022). In this regard, Lin et al. (2020), using an approach combining simulations and field plots in tropical and subtropical sites, stated that nested designs do not adequately capture forest attributes such as forest structure or tree species richness.

However, some NFIs using nested designs, such as the Spanish NFI (SNFI), use additional field measurements to identify all tree species, regardless of tree size and position within the plot (Alberdi et al. 2016; Bravo-Oviedo et al. 2021), whereas other countries, such as Japan, set a minimum plant size to evaluate richness across the whole plot (Kitahara et al. 2009). These additional measurements allow comparison between the nested design and "full census" in the largest NFI plot.

The main objective of this work is to quantify the effect of nested plot designs with increasing radii and diameter at breast height threshold on the observed tree species richness using the SNFI by comparing the number of tree species reported by the full census in a 25 m radius plot with tree species richness values produced with the nested design. Additionally, we aimed to identify the species that are more frequently missed in nested designs. Taking advantage of the diversity of bioclimatic conditions in Spain, we conducted this evaluation at foresttype level. Furthermore, given the importance of forest types on tree species richness, we analyzed tree species richness per plot at forest-type level (i.e., α -diversity). Building on the well-known species-area relationships and potential missed detection for infrequent tree species (Arrhenius 1921; Lin et al. 2020; Portier et al. 2022), we tested whether the nested plot design consistently results in underestimation of tree species richness in general and across different forest types.

2 Material and methods

We used the available open data for the Fourth SNFI (2008 to present) which plots are established on a 1×1 km UTM grid covering the whole forest area (Fig. 1A). The Fourth SNFI plots follow a nested or concentric design where trees are sampled according to their diameter at breast height (dbh) and position within the plot. In the SNFI, similar to other NFI, tree and shrub



Fig. 1 Location of the plots in the Fourth Spanish National Forest Inventory (2008 to 2021). The upper panel (A) refers to the tree species richness measured in the full census survey and the lower panel (B) to the forest types

species are differentiated according to their growth pattern, potential height, and number of main stems. Thus, tree species are identified, and the tree dbh is measured in four concentric circular subplots with increasing radii of 5, 10, 15, and 25 m, in which trees with a dbh \geq 7.5 cm, 12.5 cm, 22.5 cm, and 42.5 cm are sampled, respectively. Additionally, SNFI gathers information on regeneration, seedlings (individuals with 0 < height < 130 cm), and saplings (individuals with height \geq 1.3 m and dbh < 7.5 cm) within the 5 m radius subplot. Seedlings and saplings with dbh lower than 2.5 cm are grouped into four abundance classes by species: class 1 (2-4 plants in the regeneration subplot), class 2 (5–15 plants), and class 3 (more than 15 plants) while the number of saplings with height \geq 1.3 m and $2.5 \le dbh < 7.5$ cm is counted (see Moreno-Fernández et al. (2019) for more details on regeneration sampling).

Finally, the SNFI teams record the occurrence of all tree species occurring within the 25 m radius plot, regardless of tree size, i.e., without cut-off values for dbh or height, and location, that is a full census of tree species. The full census, however, does not gather information on the number of trees by species or other abundance-related metrics (Alberdi et al. 2016; Bravo-Oviedo et al. 2021).

We assigned a forest type to each plot according to the Spanish National Forest Map (MITECO 2013). However, this map included a large number of forest types, more than 70 in total. Therefore, to facilitate the interpretation of the results, we aggregated the forest types into the following broader spectrum types (Table 1): Subalpine and montane conifers (n=9888 plots), Mediterranean conifers (n=10,463 plots), Deciduous broadleaves (n=12,923 plots), Evergreen broadleaves (n=11,240 plots),

Table 1 Number of plots (Nplots), total number of sampled trees (dbh \geq 7.5 cm) per plot (Ntrees), total number of tree species (Nsp), and average number of tree species per plot (standard deviation between brackets) detected in the Rfull, R25_reg and R25 surveys. The three last columns refer to the percentage of undetected species when comparing Rfull vs R25_reg (UTS RfullvsR25_reg), Rfull vs R25 (UTS RfullvsR25), and R25_reg vs R25 (UTS RfullvsR25) (see Eq. 1)

Forest type	N plots	N trees	Nsp	Rfull	R25_reg	R25	UTS RfullvsR25_reg	UTS RfullvsR25	UTS R25_ regvsR25
SMC	9888	220,583	106	4.7 (2.5)	3.1 (1.7)	1.7 (1)	30 (24)	59 (24)	40 (29)
MC	10,463	130,428	76	3.6 (1.9)	2.6 (1.5)	1.4 (0.9)	24 (30)	57 (30)	42 (32)
DB	12,923	198,861	124	5 (2.7)	3.2 (2)	2.2 (1.5)	32 (24)	52 (26)	29 (29)
EB	11,240	121,823	106	3.9 (2.2)	2.6 (1.7)	1.6 (1.2)	29 (27)	56 (30)	37 (33)
MAC	1306	20,776	33	2 (1.6)	1.6 (1.2)	1.3 (1)	12 (22)	21 (31)	11 (25)
MAB	206	5154	36	4.7 (1.9)	3.7 (1.8)	3.2 (1.9)	24 (27)	36 (32)	16 (28)
0	2056	7178	23	1.8 (1.1)	1.2 (0.6)	1 (0.5)	20 (30)	28 (37)	12 (29)
MS	3837	53,984	101	5 (2.2)	3.6 (1.7)	2.2 (1.3)	26 (23)	53 (26)	36 (30)
Whole NFI	53,926	759,068	153	4.3 (2.5)	2.9 (1.8)	1.7 (1.2)	28 (27)	53 (29)	35 (32)

SMC Subalpine and montane conifers, MC Mediterranean conifers, DB Deciduous broadleaves, EB Evergreen broadleaves, MAC Mediterranean conifers, MAB Macaronesian broadleaves, O Open woodlands, MS mixed stands of conifers and broadleaves

Macaronesian conifers (n=1306 plots), Macaronesian broadleaves (n=206 plots), Open woodlands (n=2056 plots), and Mixed stands of conifers and broadleaves (n=3837 plots) (see Table 3 in Appendix for the forest

in the *i*-th plot is defined as a species found in the Rfull survey but not captured by R25_reg. Then, the percentage of undetected tree species (UTS RfullvsR25_reg_i) in the *i*-th plot is defined as follows:

UTS RfullvsR25reg_i (%) =
$$100 \frac{(\text{RichnessRfull}_i - \text{RichnessR25}_{reg_i})}{\text{RichnessRfull}_i}$$
 (1)

type aggregation). Hence, the data set comprised a total of 53,926 plots (Fig. 1B).

For each Fourth SNFI plot, we calculated the tree species richness in the four concentric subplots (R5, R10, R15, R25) for adult trees (trees with dbh \geq 7.5 cm) as well as in the regeneration subplot (Rreg). We also estimated the tree species richness by combining the species occurring in each of the four subplots with the regeneration subplot (R5_reg, R10_reg, R15_reg, R25_reg). Furthermore, we calculated the actual tree species richness (Rfull) using the full census of tree species in the plot.

We used the Wilcoxon test for paired data (Wilcoxon 1945) to investigate whether there is any significant difference between Rfull and R25_reg, between Rfull and R25 and between R52_reg and R25. Additionally, we derived the V-statistics as well as the *p*-value for the test. Large values of the V-statistic are an indicator of differences between variables. We selected these pairs of data as they are expected to be the most commonly used by researchers. These analyses were carried out at the country and forest-type level.

In the second step, we aim to determine the percentage of undetected species in the R25_reg dataset relative to the comprehensive Rfull survey. An undetected species where RichnessRfull_i and RichnessR25_reg_i are the tree species richness in the *i*-th plot captured by the Rfull design and R25_reg, respectively. We used the same approach for Rfull and R25 (UTS RfullvsR25) as well as for R25_reg and R25 (UTS R25_regvsR25). We calculated the mean values and standard deviation of the three UTS metrics at the forest-type level and for the complete data set.

To investigate those species whose detection is most affected by the nested design, we calculated the proportion of missing occurrences for the *j*-th species in R25_ reg (Eq. 2). In this paper, the term occurrence indicates whether a specific species is present in the plot.

Missing occurrence_j(%) =
$$100 \frac{\text{NRfull}_j - \text{NR25}_{\text{reg}_j}}{\text{NRfull}_j}$$
(2)

where NR25_reg_j and NRfull_j is the total number of occurrences of the *j*-th species for the whole array of plots when using R25_reg and Rfull, respectively. This also applies to R25 and Rfull.

We filtered those species with less than 30 occurrences in Rfull for the whole SNFI, i.e., Rfull < 30, to eliminate extremely rare species (e.g., *Salix cantabrica* Rech.fil.), species whose core distribution has not yet



Fig. 2 Box plots of tree species richness by forest type for the Fourth Spanish National Forest Inventory. Rfull is the full census of tree species regardless of the tree size. R25, R15, R10, and R5 refer to the tree species richness census for the nested plots (numbers indicate the maximum plot radius). Rreg is the census for saplings and seedlings in the 5 m regeneration subplot. "_reg" indicates a combined census of the adult-tree subplot and regeneration subplot

been sampled in the Fourth SNFI (e.g., *Abies pinsapo* Boiss.) and feral plants commonly used in arboriculture (e.g., *Cedrus* species) (see Appendix for the List of the filtered species).

Finally, we created a scattered plot of the number of occurrences versus the missing occurrence to address whether the species with high values of missing occurrence are common or rare. This scattered plot not only distinguished forest types but also considered the entire SNFI data set as a whole. Since the number of occurrences varies sharply among forest types, we scaled and centered this variable. Similarly, we plotted the scaled and centered median dbh of the sampled trees during the fieldwork of the SNFI by species and forest type versus the missing occurrence. This allows us to investigate whether the species with the highest missing occurrence percentages depicts large or low dbh. We selected the median rather than the mean as the distribution of the dbh was right-skewed.

3 Results

Forests located in northern Spain presented the highest levels of tree species richness per plot when considering the full census (Fig. 1). As regards the forest types, Deciduous broadleaves, Mixed stands of conifers and broadleaves and Subalpine and montane conifers present the highest tree species richness values (mean = 5.0 trees species per plot and standard deviation = 2.7, 5.0 ± 2.2 , 4.7 ± 2.5 , respectively). In contrast, Open woodlands, which are widespread in western Spain, displayed the lowest levels of tree species richness (1.8 ± 1.1). Forest types occurring in Inner Spain, i.e., Evergreen broadleaves and Mediterranean conifers, displayed intermediate levels of tree species richness (3.9 ± 2.2 and 3.6 ± 1.9 , respectively). Finally, the two forest types occurring in the Canary Islands, i.e., Macaronesian forest types, differed from each other in that the broadleaf forests (4.7 ± 1.9) had higher tree species richness values than the conifer forests (2.0 ± 1.6) (Table 1).

Not surprisingly, we found that more species were registered in the full census of tree species (Rfull) than in the census of the nested plots for all the forest types, although this is less evident for the Macaronesian conifer and broadleaf forests (Fig. 2 and Table 1). The paired-sample Wilcoxon test revealed large values of the V-statistics and statistically significant differences (p < 0.001) between Rfull and R25_reg, Rfull and R25, and R25_reg and R25 for all the forest types as well as (Table 2 and Fig. 3).

Table 2 *P*-values obtained and V-statistics (between brackets) from the Wilcoxon test. This test employed to assess the significance of differences between paired samples of tree species richness. See Fig. 3 for the boxplots of the differences between tree species richness

Forest type	Rfull vs R25_reg	Rfull vs R25	R25_reg vs R25
SMC	< 0.0001 (26,408,982)	< 0.0001 (41,381,330)	< 0.0001 (25,952,410)
MC	< 0.0001 (22,022,539)	< 0.0001 (42,677,488)	< 0.0001 (27,014,925)
DB	< 0.0001 (48,240,577)	< 0.0001 (66,072,049)	< 0.0001 (29,518,086)
EB	< 0.0001 (28,721,884)	< 0.0001 (47,406,939)	< 0.0001 (25,708,035)
MAC	< 0.0001 (59,685)	< 0.0001 (114,960)	< 0.0001 (35,511)
MAB	< 0.0001 (9180)	< 0.0001 (13,366)	< 0.0001 (2628)
0	< 0.0001 (261,594)	< 0.0001 (377,100)	< 0.0001 (55,611)
MS	< 0.0001 (3,837,753)	< 0.0001 (6,208,919)	< 0.0001 (3,799,146)
NFI	< 0.0001 (737,262,068)	< 0.0001 (1,154,853,127)	< 0.0001 (599,151,036)

SMC Subalpine and montane conifers, MC Mediterranean conifers, DB Deciduous broadleaves, EB Evergreen broadleaves, MAC Mediterranean conifers, MAB Macaronesian broadleaves, O Open woodlands, MS mixed stands of conifers and broadleaves, NFI complete Spanish National Forest Inventory





Fig. 3 Difference in tree species richness (number of tree species per plot) between the Rfull and R25_reg, Rfull and R25, and R25_reg and R25. SMC Subalpine and montane conifers, MC Mediterranean conifers, DB Deciduous broadleaves, EB Evergreen broadleaves, MAC Macaronesian conifers, MAB Macaronesian broadleaves, O Open woodlands, MS mixed stands of conifers and broadleaves, NFI complete Spanish National Forest Inventory. See Table 3 in Appendix for the results of the Wilcoxon test

The percentage of undetected species in the R25_reg dataset relative to the comprehensive Rfull survey (UTS RfullvsR25_reg) ranged from 12% (Macaronesian conifers) to 32% (Deciduous broadleaves) while the percentage was 28% for the SNFI dataset as a whole (Table 1). This suggests that R25_reg underestimated tree species richness by around 28% in comparison to Rfull. These values increased for the Rfull and R25 comparison (UTS RfullvsR25), ranging from 21.0 (Macaronesian conifers) to 59% (Subalpine and montane conifers) with a value of 53% for the SNFI dataset as a whole. The comparison between R25_reg and R25 (UTS R25_regvsR25) highlighted the importance of

the regeneration subplot. The exclusion of this pool led to a drop of 35% in the detected tree species for the SNFI dataset as a whole. The magnitude of the standard deviation of UTSs was around the mean values which suggests a high intra-forest type variation. The large ranges of the differences between the three types of surveys in fact, visually confirm the huge data variability (Fig. 3).

According to Fig. 2, tree species richness decreased with subplot size as expected. However, the regeneration subplot (5 m radius) accounts for a high number of tree species. Consequently, tree species richness increased considerably when considering seedlings and saplings in



Fig. 4 A Scaled and centered number of occurrences (occurrence indicates whether a specific species is present in the plot) versus the missing occurrence (Eq. 2). **B** Scaled and centered median diameter at breast height versus the missing occurrence SMC Subalpine and montane conifers, MC Mediterranean conifers, DB Deciduous broadleaves, EB Evergreen broadleaves, MAC Macaronesian conifers, MAB Macaronesian broadleaves, O Open woodlands, MS mixed stands of conifers and broadleaves, NFI complete National Forest Inventory. Rsq is the *R*², p the *p*-value, and N the number of observations

the estimation of tree species richness in the other subplots, i.e., R25_reg, R15_reg, R10_reg and R5_reg displayed higher richness values than R25, R15, R10, and R5.

The five species with the largest missing occurrence by forest type are shown in Table 4 in Appendix. We found that the percentage of missing occurrence (Eq. 2) for these species in R25 was quite high, above 84% in all cases except that of the two Macaronesian types, where the percentage dropped to 25% (Table 4 in Appendix). In accordance with Fig. 2, the percentage of undetected species decreased in R25_reg for all forest types, confirming the importance of the regeneration pool when estimating tree species richness. *Juniperus, Sorbus*, and *Salix* appear to be the least detected/sampled genera under the nested design when considering R25, even when the regeneration subplot is included, i.e., in R25_reg. As regards the number of occurrences and the missing occurrence, our results suggest negative linear but weak relationship between these two variables (Fig. 4A). In fact, the variability of the number of occurrences seems to increase when the missing occurrence ranges from 75 to 100%. The R^2 of these linear relationships ranges between 0.01 and 0.79. This relationship, however, is stronger for the two Macaronesian forest types (R^2 =0.79 and 0.44). The *p*-values were lower than 0.05 for Subalpine and montane conifers, Mediterranean conifers, and Macaronesian conifers. All of this indicates that uncommon species tend to be more omitted when the full design is not used although this trend is not strong.

Finally, we found a stronger and negative relationship between the median diameter of the tree species and the missing occurrence for all the forest types as well as for the complete SNFI (Fig. 4B). In this case, the R^2 ranges from 0.11 to 0.78 with the Macaronesian forest types displaying the lower values of this statistics. In this line, the *p*-value was lower than 0.001 for all the forest types with the exception of the two Macaronesian forest types. This point towards that unsampled species display low diameters.

4 Discussion

National Forest Inventories are one of the most important sources of information for forest stock estimation as well as biodiversity assessment (Chirici et al. 2011). Several countries employ nested designs to reduce sampling effort during the field task. However, to our knowledge, this is the first attempt to evaluate the impact of this type of design, combining different plot sizes and dbh thresholds, on tree species richness using NFI data. This information in Europe is requested and reported in the criteria for sustainable forest management under the "Indicator 4.1. Tree species composition" of the State of Europe's Forests of Forest Europe (Forest-Europe 2015) and, according to our results, calculating tree species richness from nested designs can result in an underestimation of the value per plot compared to the value obtained using a more thorough method, i.e., full census regardless of tree diameter. The trend found in this study remained constant among the different forest types, highlighting the consistency of our results. Furthermore, this finding agrees with the conclusions drawn by Lin et al. (2020) in their research on tropical and subtropical forests. The positive association between sampling subplot size and tree species richness found in this study is supported by the well-characterized species-area relationship (Arrhenius 1921; Condit et al. 1996) and rarefaction curves (Portier et al. 2022).

In agreement with the results obtained by Lin et al. (2020), we found that species that are more frequently omitted during the surveys of the nested designs tend to have smaller diameters. This phenomenon is particularly conspicuous in Open woodlands, where dominant trees are often overmature and have large diameters while companion species are extracted or heavily browsed before reaching large diameters (Moreno-Fernández et al. 2019). All of this helps to explain the improvement found in the estimation of tree species richness per plot when the regeneration subplot is included in the nested plot design. In this subplot, the dbh is not a constraint for tree sampling, allowing small species to be recorded. Therefore, increasing the size of the regeneration subplot could result in higher species richness estimates. However, the process of measuring seedlings and saplings is inherently time-consuming and would inevitably lead to a rise in economic costs (Alberdi et al. 2010). Most of these species with the largest values of missing occurrence (Table 4 in Appendix) appear as companion/subordinate or transient species (sensu Grime (1998)) rather than dominant species but they are not uncommon in Spanish forests (MITECO 2013). The reason is that even the number of occurrences and missing occurrences have a negative but not strong relationship between both variables but lower dbh which has a greater relationship is typical of companion species. Furthermore, species included in the Table 4 in Appendix rarely reach large dbh, which limits their inclusion in the nested sampling, as stated by Lin et al. (2020). However, many of these subordinate species, such as Sorbus and Juniper, supply fresh fruit and/or berry-like cones to mammals and birds (Santos et al. 1999; Guitián and Munilla 2010), which highlights their importance in ecosystem functionality. In addition, some of these species (see Taxus baccata in Central Spain) are afforded a protected status of some description at the regional level. Similarly, transient species such as Acacia dealbata emerged as one of the least sampled species in the Subalpine and montane coniferous forest type. Acacia species are important as they have a strong invasive behavior in northern Spain (Hernández et al. 2014; Lara-Romero et al. 2022). Hence, tree species data obtained from nested-design NFIs do not allow reliable monitoring of some endangered and invasive species. Furthermore, this data can bias species distribution models as it underestimates species occurrences. In such cases, it is strongly recommended that records from the full sampling design must be used where available. However, if abundance metrics, such as basal area or tree density are the target variables of the study, then the full sampling design cannot be employed and the only alternative is to use the information from the nested design.

The spatial pattern of tree species richness found here differs from the spatial pattern of woodland shrub richness identified in previous research (Moreno-Fernández et al. 2021). The lowest values for shrub richness are observed in the Northern Spanish forests, where tree species richness is the highest. However, this trend differs in forests with Mediterranean conditions. Moreover, it should be noted that greater tree species richness in plots located in Northern Spain does not necessarily indicate a higher total number of tree species in the region as a whole. In this regard, Portier et al. (2022) compared tree species richness metrics for five European countries and found that Spain had the lowest number of tree species per plot but the highest value for total tree species. However, we relied on the Fourth SNFI, which is not yet completed, so some provinces in southern Spain have not been sampled. This circumstance could lead to potential bias in the calculation of overall tree species diversity (γ -diversity).

5 Conclusion

National Forest Inventories provide a powerful tool to identify tree species richness in forest ecosystems. Our results, however, confirm that nested plot designs combining different dbh thresholds and plot sizes underestimate tree species richness with respect to the full census of trees being the small diameter species particularly prone to omission, suggesting a critical consideration for future biodiversity and conservation efforts. Therefore, despite of the true number of species in a given area is unknown and the sampling methods are just an approximation to the truth, we recommend the use and implementation of the full census of tree species for a more reliable estimation of tree species richness at the plot level. In the absence of the complete census inventory, we recommend incorporating data from the regeneration compartment, which hosts high levels of tree species diversity.

Appendix

Table 3 Forest type aggregation

Spanish forest map forest type	Aggregated forest type	
Tree less	Tree less (removed)	
Fagus sylvatica forests	Deciduous broadleaves	
Abies alba forests	Subalpine and montane conifers	
Autochtonous mixed forests in the Atlantic region	Deciduous broadleaves	
Quercus robur and Q. petraea forests	Deciduous broadleaves	
Juniperus phoenicea forests	Mediterranean conifers	
Juniperus spp. forests	Mediterranean conifers	
Betula spp. forests	Deciduous broadleaves	
llex aquifolium forests	Evergreen broadleaves	
Corylus avellana forests	Deciduous broadleaves	
Quercus humilis forests	Deciduous broadleaves	
Quercus pyrenaica forests	Deciduous broadleaves	
Quercus faginea forests	Evergreen broadleaves	
Quercus canariensis forests	Evergreen broadleaves	
Quercus ilex forests	Evergreen broadleaves	
Quercus suber forests	Evergreen broadleaves	
Juniperus thurifera forests	Mediterranean conifers	
Pinus sylvestris forests	Subalpine and montane conifers	
Pinus uncinata forests	Subalpine and montane conifers	
Pinus pinea forests	Mediterranean conifers	
Pinus halepensis forests	Mediterranean conifers	
Pinus nigra forests	Subalpine and montane conifers	
Pinus canariensis forests	Macaronesian conifers	
Abies pinsapo forests	Mediterranean conifers	
Castanea sativa forests	Deciduous broadleaves	
Autochtonous mixed forests in the Atlantic region	Evergreen broadleaves	

Table 3 (continued)

Spanish forest map forest type	Aggregated forest type
Riparian forests	Deciduous broadleaves
Open woodlands	Open woodlands
<i>Olea europaea</i> forests	Evergreen broadleaves
Macaronesian rainforests	Macaronesian broadleaves
Palm tree stands	Evergreen broadleaves
Productive plantations	Subalpine and montane conifers
Mixtures of autochthonous and allochthonous boradleaves	Deciduous broadleaves
Arbutus unedo forests	Evergreen broadleaves
Populus and Platanus plantations	Deciduous broadleaves
Plantations of allochthonous conifer species	Subalpine and montane conifers
Invasive species	Deciduous broadleaves
Juniperus phoenicea spp turbinata forests	Macaronesian conifers
<i>Myrica faya</i> and <i>Erica</i> spp. Forests	Macaronesian conifers
<i>Ceratonia siliqua</i> forests	Evergreen broadleaves
Autochthonous mixed forests of broadleave species in the Atlantic region	Deciduous broadleaves
Other Macaronesian native broad- leaves	Macaronesian broadleaves
Fraxinus spp. forests	Deciduous broadleaves
Eucalyptus forests	Evergreen broadleaves
Pinus radiata forests	Subalpine and montane conifers
<i>Pinus pinaster</i> in the Mediterranean region	Mediterranean conifers
Pinus pinaster in the Atlantic region	Subalpine and montane conifers
Quercus rubra forests	Deciduous broadleaves
Other allochthonous conifers in production	Subalpine and montane conifers
Mixtures of autochthonous and allochthonous conifers	Subalpine and montane conifers
Mixtures of autochthonous and allochthonous conifers	Mixed stands of conifers and broadleaves
Autochtonous mixed forests of conifers in the Alpine region	Subalpine and montane conifers
Autochtonous mixed forests of conifers in the Atlantic region	Subalpine and montane conifers
Autochtonous mixed forests of conifers in the Mediterranean region	Mediterranean conifers
Autochtonous mixed forests of conifers in the Macaronesian region	Macaronesian conifers
Autochtonous mixed forests of conifers and broadleaves in the Alpine region	Mixed stands of conifers and broadleaves
Autochtonous mixed forests of conifers and broadleaves in the Atlantic region	Mixed stands of conifers and broadleaves
Autochtonous mixed forests of conifers and broadleaves in the Mediterranean region	Mixed stands of conifers and broadleaves

Table 3 (continued)

Spanish forest map forest type	Aggregated forest type
Autochtonous mixed forests of conifers and broadleaves in the Macaronesian region	Mixed stands of conifers and broadleaves
Open forests of broadleaves	Open woodlands
Open forests of conifers	Open woodlands
Open forests of conifers and broad- leaves	Open woodlands
Reforestations of unknown species	Subalpine and montane conifers

List of the species with less than 30 records in the full census.

Abies pinsapo Boiss. Ailanthus altissima (Mill.) Swingle. Carpinus betulus L. Cedrus atlantica (Endl.) Manetti ex Carriere. Cedrus deodara (Lamb.) G.Don. Cedrus libani A.Rich. Crataegus azarolus L. Crataegus laciniata Besser. Cupressus lusitanica Mill. Cupressus macrocarpa Hartw. ex Gordon. Dracaena draco (L.) L. Erica scoparia L. Eucalyptus robusta Sm. Eucalyptus viminalis Labill. Fraxinus ornus L. Heberdenia bahamensis (Lam.) Sprague. Ilex platyphylla Webb & Berthel. Juglans nigra L. Juniperus cedrus Webb & Berthel. *Larix x eurolepis* A.Henry. Morus alba L. *Morus* spp. Morus nigra L. Pistacia atlantica Desf. Platanus orientalis L. Pleiomeris canariensis (Willd.) A.DC. Prunus lusitanica L. Prunus padus L. Quercus canariensis Willd. Quercus lusitanica Lam. Rhamnus glandulosa Aiton. Rhus coriaria L. Salix babylonica L. Salix canariensis C.Sm. ex Link. Salix cantabrica Rech.fil. Sophora japonica L.

Sorbus chamaemespilus (L.) Crantz. Tamarix canariensis Willd. Tetraclinis articulata (Vahl) Mast. Thuja spp. Ulmus pumila L. Visnea mocanera L.fil.

Table 4 Percentage of the five most unsampled species in the 25 m radius nested plot with and without considering the regeneration subplot (R25 and R25_reg, respectively)

Forest type	R25	R25_reg
Subalpine and mon- tane conifers	Pyrus sp (98.2) Corylus avellana (97.2) Sorbus domestica (97.1) Juniperus communis (96.9) Acacia dealbata (96.9)	Acacia dealbata (84.4) Tilia platyphyllos (76.7) Sorbus domestica (74.3) Sambucus nigra (71.5) Taxus baccata (70.5)
Mediterranean conifers	Celtis australis (100) Crataegus monogyna (98.9) Sorbus torminalis (98.5) Sorbus aria (98.1) Sorbus aucuparia (84.9)	Ficus carica (87.3) Salix atrocinerea (84.9) Ulmus minor (82.3) Sorbus aucuparia (84.9) Salix sp. (81.0)
Deciduous broad- leaves	Juniperus phoenicea (100) Juniperus communis (97.0) Salix purpurea (95.2) Crataegus laevigata (94.5) Juniperus oxycedrus (92.1)	Juniperus phoenicea (84.9) Taxus baccata (65.1) Pinus halepensis (65.9) Olea europea (68.9) Ficus carica (73.1)
Evergreen broadleaves	Juniperus communis (97.6) Pyrus sp. (97.4) Sorbus domestica (97.3) Laurus nobilis (95.3) Juniperus phoenicea (95.1)	Ficus carica (75.3) Sorbus aucuparia (73.0) Pyrus sp. (68.4) Sorbus domestica (67.6) Salix alba (66.7)
Macaronesian conifers	Prunus sp. (91.2) Ficus carica (90.1) Castanea sativa (79.5) Persea indica (69.0) Erica arborea (52.4)	Castanea sativa (79.5) Ficus carica (78.1) Prunus sp. (73.5) Persea indica (38.1) Pinus radiata (36.1)
Macaronesian broad- leaves	Picconia excelsa (69.2) Prunus sp. (53.3) Erica arborea (31.0) Persea indica (27.4) Myrica faya (24.2)	Picconia excelsa (48.1) Prunus sp. (40.0) Erica arborea (20.3) Persea indica (19.2) Myrica faya (15.4)
Open woodlands	Castanea sativa (100) Pyrus spp. (98.6) Crataegus monogyna (98.4) Quercus robur (95.0) Eucalyptus globulus (93.8)	Castanea sativa (78.8) Pyrus spp. (77.1) Crataegus monogyna (74.1) Eucalyptus globulus (60.4) Olea europaea (60.2)

Table 4 (continued)

Forest type	R25	R25_reg	
Mixed stands of coni- fers and broadleaves	Pyrus spp. (96.5) Juniperus communis (96.3) Juniperus phoenicea (93.7) Crataegus monogyna (93.6) Corylus avellana (91.1)	Malus sylvestris (76.7) Prunus avium (66.1) Sambucus nigra (64.9) Salix atrocinerea (64.1) Sorbus aucuparia (63.6)	
Complete Fourth Spanish National For- est Inventory	Sorbus domestica (97.5) Juniperus communis (97.3) Salix purpurea (96.8) Crataegus laeviagata (95.2) Pyrus spp. (94.8)	Ficus carica (78.9) Sorbus domestica (76.1) Fraxinus spp. (68.3) Malus sylvestris (64.4) Taxus baccata (64.2)	

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Authors' contributions

Conceptualization: Iciar Alberdi and Laura Hernández; methodology: Daniel Moreno-Fernández; formal analysis and investigation: Daniel Moreno-Fernández; writing—original draft preparation: Daniel Moreno-Fernández; writing review and editing: Iciar Alberdi, Isabel Cañellas, Patricia Adame and Laura Hernández; funding acquisition: Iciar Alberdi and Isabel Cañellas; resources: Patricia Adame. The authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated during and/or analyzed during the current study are available in the Portal de Datos e Inventario del MITECO repository, https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional/cuarto_inventario.html

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no competing interests.

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