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Where are Europe's last primary forests?

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Abstract

Aim: Primary forests have high conservation value but are rare in Europe due to historic land use. Yet many primary forest patches remain unmapped, and it is unclear to what extent they are effectively protected. Our aim was to (1) compile the most comprehensive European-scale map of currently known primary forests, (2) analyse the spatial determinants characterizing their location and (3) locate areas where so far unmapped primary forests likely occur.

Location: Europe.

Methods: We aggregated data from a literature review, online questionnaires and 32 datasets of primary forests. We used boosted regression trees to explore which biophysical, socio-economic and forest-related variables explain the current distribution of primary forests. Finally, we predicted and mapped the relative likelihood of primary forest occurrence at a 1-km resolution across Europe.

Results: Data on primary forests were frequently incomplete or inconsistent among countries. Known primary forests covered 1.4 Mha in 32 countries (0.7% of Europe's forest area). Most of these forests were protected (89%), but only 46% of them strictly. Primary forests mostly occurred in mountain and boreal areas and were unevenly distributed across countries, biogeographical regions and forest types. Unmapped primary forests likely occur in the least accessible and populated areas, where forests cover a greater share of land, but wood demand historically has been low.

Main conclusions: Despite their outstanding conservation value, primary forests are rare and their current distribution is the result of centuries of land use and forest management. The conservation outlook for primary forests is uncertain as many are not strictly protected and most are small and fragmented, making them prone to extinction debt and human disturbance. Predicting where unmapped primary forests likely occur could guide conservation efforts, especially in Eastern Europe where large areas of primary forest still exist but are being lost at an alarming pace.

KEYWORDS

boosted regression trees, forest naturalness, land-use change, old-growth forest, primary forest, spatial determinants, sustainable forest management, virgin forest

1 | INTRODUCTION

Primary forests are becoming rare as forestland globally is cleared for agriculture or put under active management (Mackey et al., 2015; Potapov et al., 2017). Primary forests, according to the Food and Agricultural Organization (FAO), refer to naturally regenerated forests of native species where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed (FAO, 2015). Given their irreplaceability and unique qualities, protecting primary forests is a global concern (Mackey et al., 2015). Not only are primary forests cherished for their wild nature (Navarro & Pereira, 2012), and represent a social perception of untouched nature (Schnitzler, 2014), but they are also ecologically important in regions where forests are highly fragmented (Vandekerkhove, De Keersmaeker, Menke, Meyer, & Verschelde, 2009). Primary forests, for instance, serve as refuges or sources of propagules for rare or endangered species, especially for forest species sensitive to human disturbance (Paillet et al., 2015; Peterken, 1996). Furthermore, primary forests serve as a model for understanding natural disturbance and successional dynamics (Král, McMahon, Janík, Adam, & Vrška, 2014; Kuuluvainen & Aakala, 2011; Leibundgut, 1959), especially in the face of climate change, and provide baselines for the delivery of ecosystem services under unmanaged conditions, including carbon stocks and sequestration (Burrascano, Keeton, Sabatini, & Blasi, 2013; Harmon, Ferrell, & Franklin, 1990). Finally, primary forests help us to evaluate human impacts on forest ecosystems and to understand the potential and limitations of close-to-nature forest management (Bauhus, Puettmann, & Messier, 2009; EEA, 2014; Kuuluvainen & Aakala, 2011).

In Europe, as in other human-dominated regions, historical deforestation and forest exploitation came close to eliminating primary forests (Kaplan, Krumhardt, & Zimmermann, 2009; Potapov et al., 2017). Europe's forests are now mainly composed of seminatural forests, while forests undisturbed by man account for only 4% of the total (FOREST EUROPE, 2015). Even this little share of undisturbed forest is heavily fragmented as virtually no intact forest landscapes >500 km^2 exist outside European Russia and boreal northern Europe (Potapov et al., 2017). Finally, although some Eastern European countries may still contain relatively large areas of primary forests (Frank et al., 2007; Kulakowski et al., 2017), these remain often unmapped and unprotected and are being lost at an alarming rate (Chylarecki & Selva, 2016; Knorn et al., 2013; Mikoláš et al., 2017).

Seminatural forests cannot be easily restored to a primary status (Ford & Keeton, 2017). In the absence of anthropogenic disturbance, forests slowly recover the natural disturbance dynamics and develop those structural features (e.g., deadwood, large live trees and presence of canopy openings of various sizes) that are typical for the old-growth phases of primary forests, although this process takes decades (Burrascano et al., 2013; Paillet et al., 2015; Vandekerkhove et al., 2009). The ongoing process of agricultural intensification in productive areas, which co-occurs with deintensification or even abandonment of marginal areas, may offer important conservation opportunities (Jepsen et al., 2015; Navarro & Pereira, 2012; Schnitzler, 2014). In many Western European countries, satisfying wood demands increasingly relies on imports, while forests located in remote areas are today being managed much less intensively than in the past (Burrascano et al., 2016; Navarro & Pereira, 2012). As a result of these economic changes, as well as of changing management priorities, the proportion of European forests in the older-age classes is increasing, although wide regional differences exist (FOREST EUROPE, 2015). Efforts devoted at identifying and protecting primary forests should also include late-successional forests, especially given that in many European regions, these forests represent the most natural forests still existing in the landscape. Late-successional forests play an important role in terms of biodiversity conservation, ecological functioning and provisioning of ecosystem services.

For the purpose of this study, we use the term "*primary forests*," to include all forests having a high naturalness, without implying that these forests were never cleared nor disturbed by man, which is in line with the FAO definition of primary forests (Buchwald, 2005; FAO, 2015). Research on the structure and dynamics of primary forests in Europe has a long tradition (Leibundgut, 1959). For instance, strictly protected forest areas were in the focus of two large collaborative efforts to coordinate, harmonize and link research on forest reserves (Diaci, 1999; Frank et al., 2007; Parviainen, 2000). A growing body of knowledge has accumulated ever since (Burrascano et al., 2013; EEA, 2014; Keeton et al., 2010; Kuuluvainen & Aakala, 2011), including data on the most iconic primary forests, such as Białowieża in Poland, Uholka-Shyrokyi Luh in Ukraine, Žofín in the Czech Republic and Izvoarele Nerei in Romania (Bernadzki, Bolibok, Brzeziecki, Zajączkowski, & Zybura, 1998; Hobi, Commarmot, & Bugmann, 2015; Král et al., 2014; Veen et al., 2010). Nevertheless, only a few countries have systematically inventoried remaining primary forest fragments (e.g., Adam & Vrška, 2009) aside from forest reserves and internationally recognized primary forest patches. Large regional gaps thus remain, especially in those countries where the political resistance to the designation of additional strict reserves is hindering efforts to identify remaining primary forest (Mackey et al., 2015). Furthermore, transboundary efforts for mapping and protecting primary forests are rare and confined to specific ecoregions (e.g., the Carpathians, the green belt of Fennoscandia) or forest types (e.g., UNESCO network of primeval beech forests).

Despite these past efforts for consolidating and harmonizing information at the continental scale (Diaci, 1999; Frank et al., 2007; Parviainen, 2000), no up-to-date and spatially detailed European-wide database and map of primary forests are currently available (García Feced, Berglund, & Strnad, 2015). As a result, systematic research to quantify the extent of primary forests in Europe, to assess whether primary forests are adequately protected or to understand what determines their spatial distribution is missing. A map of the primary forests of Europe is thus highly needed, to ensure that primary forests receive adequate recognition and protection (Mackey et al., 2015) and as a starting point for a systematic gap analysis that highlights those biogeographical regions or forest types for which primary forests are absent or underrepresented. Such a map is increasingly needed in the light of international commitments, such as the European Biodiversity Strategy (Target 3b - Action 12, which calls for Member States to ensure the preservation of wilderness areas) or the EU's Green Infrastructure Strategy, to ensure that primary forests and the ecosystem services they provide can be protected. Finally, analysing the determinants of the spatial distribution of primary forests could help to identify the socio-economic drivers (e.g., bioenergy production) behind the threats faced by these forests (e.g., illegal logging and anthropogenic wildfires), as well as candidate sites for restoration initiatives, for instance where land-use pressure and opportunity-cost of restoration are decreasing (Navarro & Pereira, 2012; Schnitzler, 2014).

In this paper, we addressed the following questions:

1. What is the currently known distribution of primary forests across Europe, biogeographical regions, forest types and protection levels?

TABLE 1 Description of predictors used to model the likelihood of finding previously unmapped primary forests. For each predictor, we reported the measurement unit, resolution (Res), data source, the sign of the expected relationship with the likelihood of occurrence of primary forests (+ positive, −negative), and data format. (R—raster, V—vector). Only underlined variables were retained in the final model

Class	Predictor	Description	Mes. Unit	Res	Source	Expected relationship	Format
Climate	*Growing degree days (GDD)*	Number of days per year having a mean temperature >5°C	Days	30 arc s	Hijmans, Cameron, Parra, Jones, and Jarvis (2005)	−	R
	Mean annual temperature	Long-term mean annual temperature	°C	30 arc s	Hijmans et al. (2005)	−	R
	Water availability	Priestly–Taylor coefficient: difference between precipitation and potential evapotranspiration	Ratio	30 arc s	Trabucco and Zomer (2010)	+	R
Soil	*Crop suitability*	Maximum suitability value across 16 crops	0–1	30 arc s	Zabel, Putzenlechner, and Mauser (2014)	−	R
Topography	Elevation	Elevation a.s.l.	m	30 arc s	NASA, (2006)	+	R
	Slope		%	30 arc s	NASA, (2006)	+	R
	Aspect			30 arc s	NASA, (2006)	±	R
	Ruggedness	Terrain ruggedness expressing relief energy	m	30 arc s	NASA, (2006)	+	R
	Solar radiation	Potential annual direct incident radiation	log (MJ/cm^2 *year)	1 km	McCune and Keon (2002)	−	R
Forest conditions	*Forest cover*	Percentage of forested area	%	1 km	Kempeneers, Sedano, Seebach, Strobl, and San-Miguel-Ayanz (2011)	+	R
	Forest core area	Percentage of forested area classified as core	%	1 km	Soille and Vogt (2009)	+	R
	Growing stock		m^3/ha	1 km	Gallaun et al. (2010)	+	R
	Net annual increment	Annual aboveground biomass increment	Ton d.m.* per ha*year	1 km	Busetto, Barredo, and San-Miguel-Ayanz (2014)	−	R
	Biogeographical region		Dummy		BfN, (2003)		V
Socio-economic	*Population density*	Landscan dataset	n/km^2	30 arc s	Oak Ridge National Laboratory, (2005)	−	R
	Travel time to the nearest city	Estimated travel time to the nearest city of 50,000 or more people in the year 2000	Min	1 km	Nelson (2008)	+	R
	Harvest intensity (2000–2015 average)	Percentage of net annual increment harvested in (2000-2015 average)	%	Country	FOREST EUROPE (2015)	−	V
Historical legacies	*Forested cover (1850)*	Amount of land suitable for agriculture still forested in 1850	%	Country	Kaplan et al. (2009)	+	V
	Wood demand (1828)	Historical wood demand reconstructed for the year 1828	TgC	0.5°	McGrath et al. (2015)	−	R

2. Which biophysical, socio-economic historical land-use factors determine the extant pattern of primary forests?
3. What are the areas with the highest likelihood of finding previously unmapped primary forests?

2 | METHODS

2.1 | Primary forest database

To produce the first map of known European primary forests, we adopted FAO definition of primary forests (FAO, 2015). We followed the framework proposed by Buchwald (2005), according to which the term primary forest comprises all those forests previously indicated as primeval, virgin, near-virgin, old-growth and long-untouched (i.e., classes n10 to n5 in Buchwald, 2005 — see Supporting Information Appendix S1—for definitions). Here, we embrace a positivist perspective implying that empirical evidence can be used to infer whether forests have been impacted by human activities within the last two centuries.

Based on this set of conceptual definitions, we conducted a literature review and collected all the studies published between January 2000 and January 2017, reporting basic information on primary forests in Europe, excluding Russia. We limited our review to papers published after 2000, to avoid including those forests that, although being reported as primary in older papers, may have meanwhile lost their primary status due to human disturbance. We identified relevant publications in the ISI Web of Knowledge using the search term "(primary OR virgin OR old-growth OR primeval) AND forest*" in the title field. We conservatively avoided other terms such as "unmanaged" (=not under active management), "natural" (=stocked with naturally regenerated native trees) or "ancient" (=never cleared for agriculture). Although widely used in the European literature, these concepts represent necessary but not sufficient conditions for considering a forest as primary for our paper.

The initial search was then refined using geographical and subject areas as filters (see Supporting Information Appendix S2 for details). This preliminary list of papers was then supplemented with the literature in their own reference lists as well as with studies known to the authors. For all papers, we extracted the location and basic information on the primary forests described. In addition, we sent out a questionnaire to scientists and experts on primary forests to collect information on (1) existing maps and databases of primary forests in their country, (2) primary forests not yet included in existing maps and databases, and (3) contacts of additional experts. In total, we contacted 134 forest experts from 33 European countries (Supporting Information Table S1). After finding a suitable dataset or map, we invited the data owner to join our informal research network and share the dataset in their possession. To avoid terminological inconsistencies, the inclusion of a country dataset was conditional on the establishment of an explicit equivalence between country-specific definitions and the definition framework of Buchwald (2005).

We integrated all data into a geodatabase, where each primary forest patch was reported either as a polygon or as a point location. Our minimum mapping unit was two ha. For each forest, we gathered a set of basic descriptors, including name, location, naturalness level (following the broad definitions reported in Buchwald, 2005—Supporting Information Appendix S1), extent and dominant tree species. We assigned each stand to a broad forest type, based on the stand's dominant tree species, elevation and biogeographical region (BfN, 2003; EEA, 2006). We derived the protection status and IUCN category of each forest patch based on the World Database of Protected Area (UNEP-WCMC & IUCN, 2017). A detailed description of the database architecture and each dataset is in Supporting Information (Supporting Information Tables S2, S3 and Appendix S3).

2.2 | Biophysical and socio-economic location characteristics of the mapped forests

Based on the variables that were previously used as spatial determinants of harvest intensity and wood production across Europe (Levers et al., 2014; Verkerk et al., 2015), we identified a set of 19 biophysical (including climate, soil, topography and forest conditions), socio-economic and historical land-use variables that could explain primary forest distribution (Table 1). Most predictors were available as raster layers with a resolution of 1 × 1 km or finer, with the exception of three variables that either had a 0.5° resolution, or were available at the country level. We reprojected all predictors to the Lambert azimuthal equal-area projection. We checked for collinearity and excluded collinear predictors when an individual variable returned a variance inflation factor (VIF) >10 (Dormann et al., 2013) or returned a Pearson's $r > 0.7$ with another variable (in this case, the variable having the highest VIF was excluded; Table 1).

2.3 | Relative likelihood of the occurrence of undetected primary forests

We converted the map of primary forests to a 1-km presence–absence raster and used boosted regression trees (BRTs) to explore the relationships between our set of predictors and the occurrence of primary forests. In this way, we estimated the relative likelihood that a grid cell contained a primary forest patch, although we recognize that the relatively coarse scale of most predictors may weaken the performance of our model. We relied on modelling as, to our knowledge, no reliable workflow exists that allows differentiating primary from nonprimary forest using remote sensing data only.

BRTs are nonparametric models based on decision trees in a boosting framework. They have the advantage of not requiring prior assumptions and being relatively robust against overfitting, missing data, and collinearity. Therefore, BRTs represent a flexible approach for uncovering nonlinear relationships and interactions among predictors. BRTs are increasingly used for attaining system understanding, hypothesis testing and statistical inferences (Dormann et al., 2013; Elith, Leathwick, & Hastie, 2008). Our BRT was parameterized using a learning rate of

0.02, a tree complexity of 5 and a bag fraction of 0.7 (Elith et al., 2008). We used the *gbm.step* routine provided by the DISMO package (Hijmans, Phillips, Leathwick, & Elith, 2011) in R (R Development Core Team, 2017) to determine the optimal number of trees. We ran all the analyses after masking nonforest areas (Gallaun et al., 2010).

As the data on primary forest presence were spatially clustered and this may lead to inaccurate models (Phillips et al., 2009), we used a spatial filtering approach to rarefy the available data on a 5 × 5-km grid. To account for the bias in our dataset due to some countries not reporting any or very few data, we also created a map of sampling effort (1: high sampling effort, 0: low sampling effort; Supporting Information Figure S1). We then stratified the selection of 37,060 pseudo-absence points (i.e., ten times the number of presences after the rarefaction) based on the distribution of presence points in the map of sampling effort (Kramer-Schadt et al., 2013). To account for remaining spatial bias, we used the *pwdSample* function in the DISMO package to pair each test presence site with the closest test pseudo-absence site prior to evaluating the performance of our model, thus removing the remaining spatial sorting bias (Hijmans, 2012). We also tested for spatial autocorrelation in model residuals using Moran's I.

We used the receiver-operating characteristic curves (ROC) and the area under the curve (AUC) to evaluate prediction performance based on 10-fold cross-validation. As AUC is only rank-based, we also calculated Pearson's correlation between the observed presence\pseudo-absence and the likelihood predicted from the BRT model (Phillips et al., 2009). Finally, we used the true-positive and true-negative rates, to calculate model accuracy and precision when using different likelihood thresholds for discriminating between predicted primary forest occurrence vs. absence. We used the threshold returning the highest accuracy to create a map of the 1 × 1-km forested grid cell potentially containing one or more patches of primary forest. The relative importance of predictors was evaluated according to the number of times that a variable was selected for splitting, weighted by the squared improvement to the model as a result of each split and averaged over all trees (Elith et al., 2008). For those predictors with a relative importance above that expected by chance (100%/number of predictors), we produced partial dependency plots constrained between the 2.5 and 97.5 percentiles of the predictor range and smoothed using a LOESS interpolation (span parameter = 0.2) to enhance interpretability.

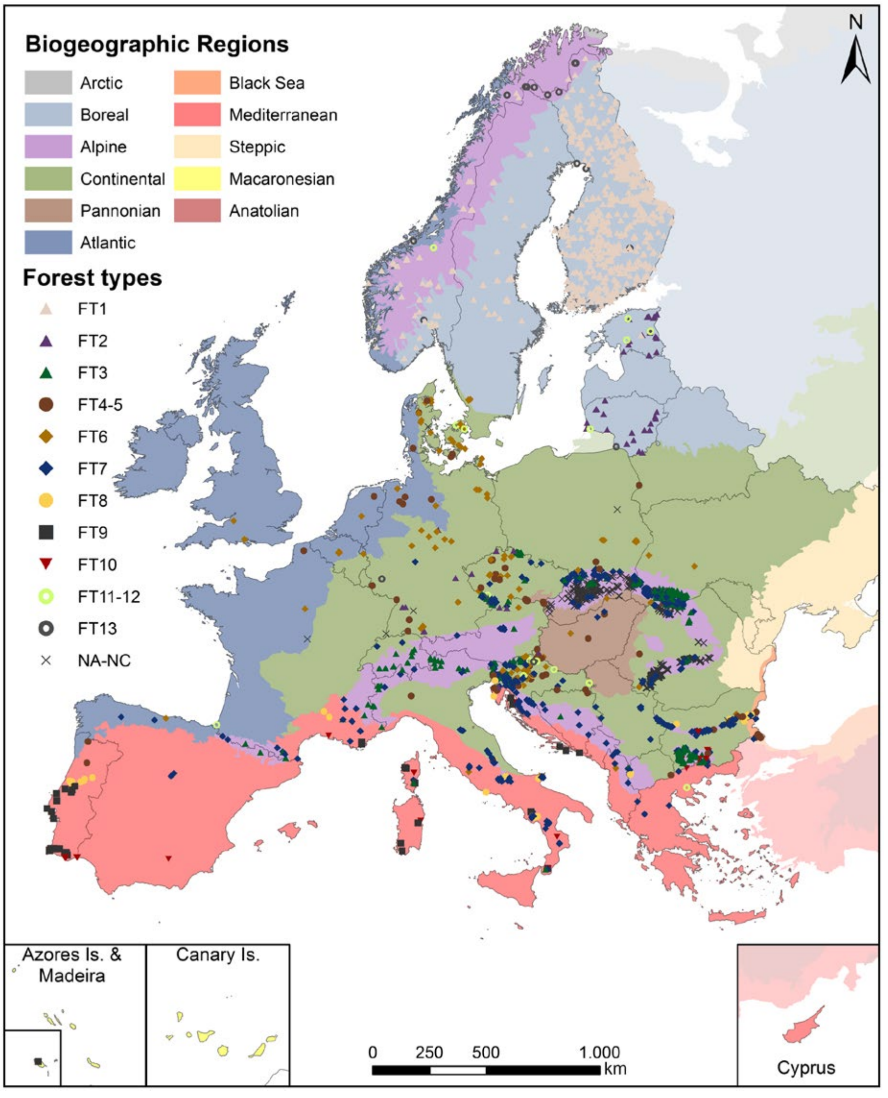

FIGURE 1 Distribution of primary forest patches retrieved for Europe by forest type. The map of biogeographical regions in the background follows BfN (2003). Forest types follow EEA (2006): FT1—boreal forest, FT2—hemiboreal and nemoral coniferous-mixed forest, FT3—alpine coniferous, FT4-5—mesophytic deciduous and acidophilus forest, FT6—beech forest, FT7—mountainous beech forest, FT8—thermophilus deciduous forest, FT9—broadleaved evergreen forest, FT10—coniferous Mediterranean forest, FT11-12—mire and swamp forests and floodplain forest, FT13—nonriverine alder, birch or aspen, NA-NC—no data/unclassified [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

Our database covered 1.4 Mha of primary forest in 32 European countries (Figure 1). This database was composed of 32 regional datasets (Supporting Information Table S3) that we integrated with data on additional 254 primary forest patches, described in 94 studies or reports retrieved through the literature review (Supporting Information Table S4). A list of the data sources is in Supporting Information Appendix S4. Most of the primary forests for which data were available were located in northern Europe, especially Finland (0.9 Mha), and Eastern Europe (0.2 Mha), especially Ukraine, Bulgaria and Romania (Supporting Information Table S5). The countries having the highest proportion of primary forest were Finland (2.9% of national territory), Switzerland, Lithuania, Slovenia and Bulgaria (each about 0.5%; Figure 2). These rankings, however, are heavily affected by the availability of data and disregard the contribution of countries for which we could not retrieve adequate data. We found complete inventories only for three countries (Czech Republic, Slovakia and Hungary) and partial or incomplete inventories for additional four countries, but either limited to specific mountain ranges (e.g., Carpathians—Romania, Ukraine) or protected areas (France, Italy; Figure 2). Countries for which we were not able to retrieve data on primary forests were Latvia, Belarus, Moldova and Ireland. For Sweden, Austria, the UK, Bosnia and Herzegovina, Montenegro and Serbia, we only found scattered information, that is very few records in the literature, but no (or very limited) spatial datasets deriving from local inventories (Figure 2). Nevertheless, we cannot exclude that additional data may exist for these or other countries that we did not manage to retrieve, especially for countries expected to host wide stretches of primary forest, such as Sweden.

Primary forests occurred mostly in the boreal (1 Mha, 1% of that biogeographical region) and the alpine regions (0.4 Mha, 0.6%). The Macaronesian region also had a high relative proportion of primary forests, all of it located in the Laurisilva of Madeira (15,100 ha, 1.5%; Supporting Information Table S6). The mapped primary forest patches were, on average, very small: The median size was only 24 ha, and only 4.3% of the patches were larger than 1,000 ha. Most (89.1%) of the primary forest in our dataset was protected, but only 46% was currently under strict protection (IUCN category I), with an additional 24% being included in national parks (IUCN category II; Figure 3, Supporting Information Table S5).

With regard to the forest types (FTs, sensu EEA, 2006), boreal forest (FT1) accounted for the highest share of the mapped primary forests (1.09 Mha), followed by mountain beech forest (FT7—0.15 Mha) and, to a minor extent, alpine coniferous forest (FT3—0.07 Mha; Figure 1, Supporting Information Figure S2). According to the definitions reported in Buchwald (2005—Supporting Information Appendix S1), most of the primary forests in our dataset were near-virgin (n7—1.20 Mha), while old-growth (n6—0.15 Mha) or long-untouched stands (n5—0.11 Mha) accounted only for a minor fraction (10%) of the cumulative area we mapped. However, when

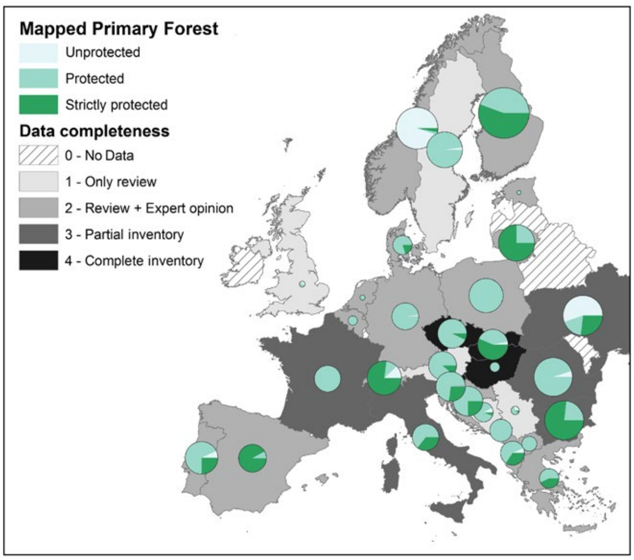

FIGURE 2 Contry-wise completeness of primary forest data and proportion of primary forest under strict protection (IUCN category I), included in protected areas having other IUCN categories or unprotected. The size of the pie is proportional to the logarithm of the total primary forest extent mapped in a country. The pie fractions only represent the data currently available and they should not be directly compared across countries, as data quality and availability differ. Furthermore, for some countries, only inventories of primary forest located either inside (e.g., Italy, Finland and France) or outside (Norway) protected areas were available [Colour figure can be viewed at wileyonlinelibrary.com]

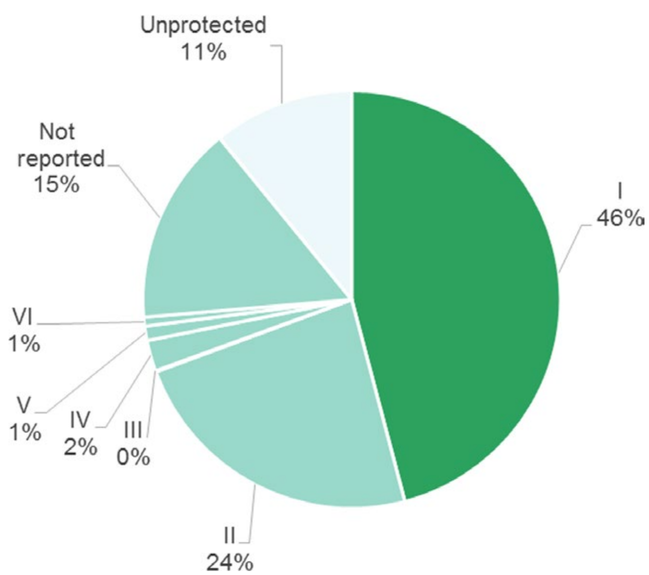

FIGURE 3 Area of European primary forest across IUCN categories. I—strict nature reserves or wilderness areas; II—national parks; III—natural monuments or features; IV—habitat/species management areas; V—protected landscapes; and VI—protected area with sustainable use of natural resources. When a patch of primary forest was protected under multiple levels, we only considered the strictest category [Colour figure can be viewed at wileyonlinelibrary.com]

considering the number of polygons rather than the area, the highest share of the forest patches we mapped were classified as old-growth forests and belonged to the boreal (FT1), alpine coniferous (FT3) and mountain beech (FT7) forest types (Supporting Information Figure S3).

The boosted regression tree modelling provided insights into the relative importance of our predictors in determining the spatial patterns of known primary forests. The BRT model fitted 2,050 trees and returned a relatively high cross-validated AUC and correlation (mean ± *SD* range 0.86 ± 0.005 and 0.63 ± 0.008, respectively). When evaluating the model performance on the test data selected to control for spatial sorting bias (Hijmans, 2012), the AUC and the correlation were lower (0.70 and 0.33, respectively), indicating that the model performance was affected by the spatial dependency of the training data. The highest model accuracy (0.64) was observed for a threshold corresponding to the 90th percentile of the probability distribution (Supporting Information Table S7, Figure S4).

Biophysical, socio-economic and historical variables all played a role in determining the likelihood of primary forest occurrence (Figure 4). Primary forests were more likely found in areas with higher ruggedness and water availability. Socio-economic factors had the highest relative importance among the selected variables, with accessibility and population density selected in 12.6% and 12.2% of all model runs. Primary forests occurred more likely farther away from major towns and where population density was lower. Both historical variables we used were important predictors: The likelihood of occurrence of primary forest decreased for increasing historical levels of wood demand up to a certain threshold, above which it increased again. The amount of land suitable for agriculture still forested in 1850, instead, showed a reverse U-shaped relationship. Finally, our model also highlighted differences across biogeographical regions: The likelihood of occurrence of primary forests was higher than average for the alpine, Black Sea and boreal regions.

The areas with the highest primary forest likelihood (Figure 5) were along the northern Finnish–Russian border, in the Finnish–Swedish border and in mountain ranges, especially the Carpathians, the eastern Alps, the Dinaric Mountains and, to a lesser extent,

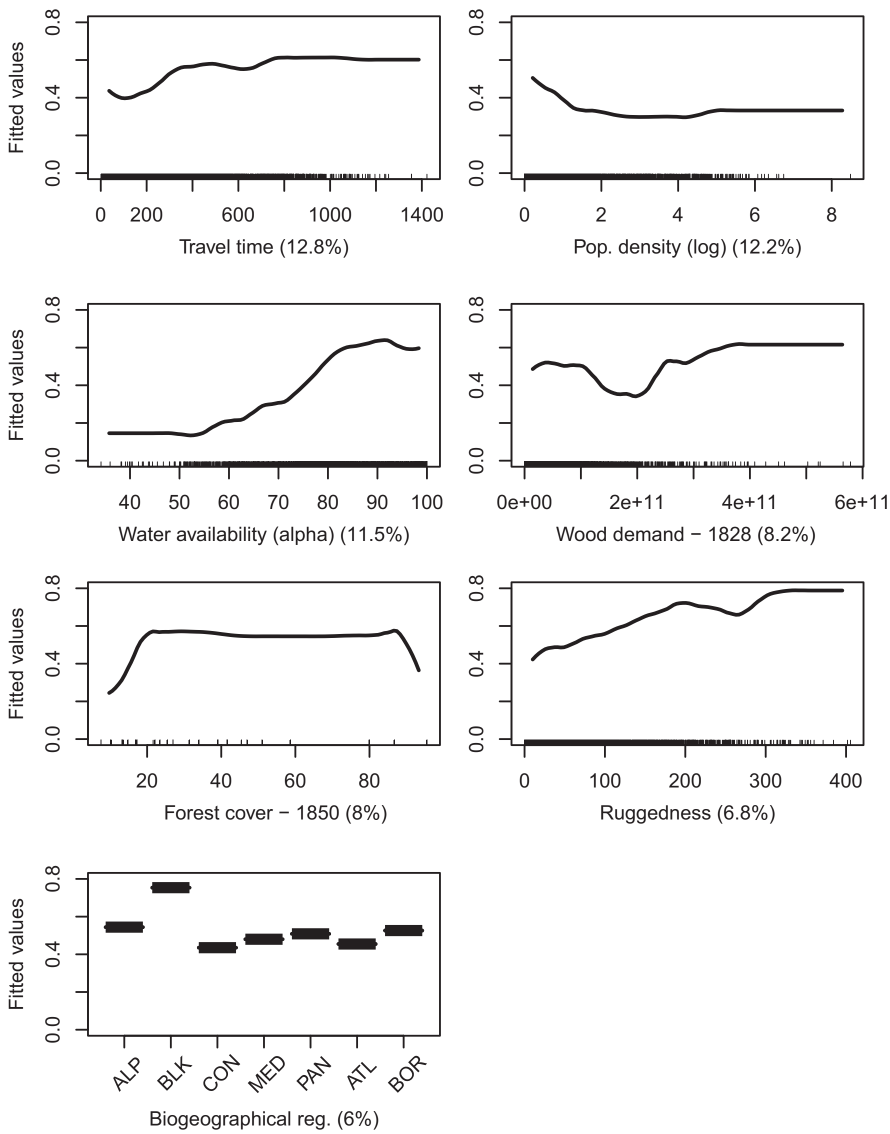

FIGURE 4 Partial dependency plots (PDPs) showing the relationship between spatial determinants and the relative likelihood of occurrence of primary forest patches in a given 1 × 1-km pixel. The vertical axis of the PDPs shows fitted values for each observation along the variable's data range (horizontal axis). X-axes are equipped with rug plots that visualize the distribution of the respective data space. Numbers in parentheses represent the relative importance of a given variable. Biogeographical regions: ALP = alpine, BLK = Black Sea, CON = continental, MED = Mediterranean, PAN = Pannonian, ATL = Atlantic, BOR = boreal)

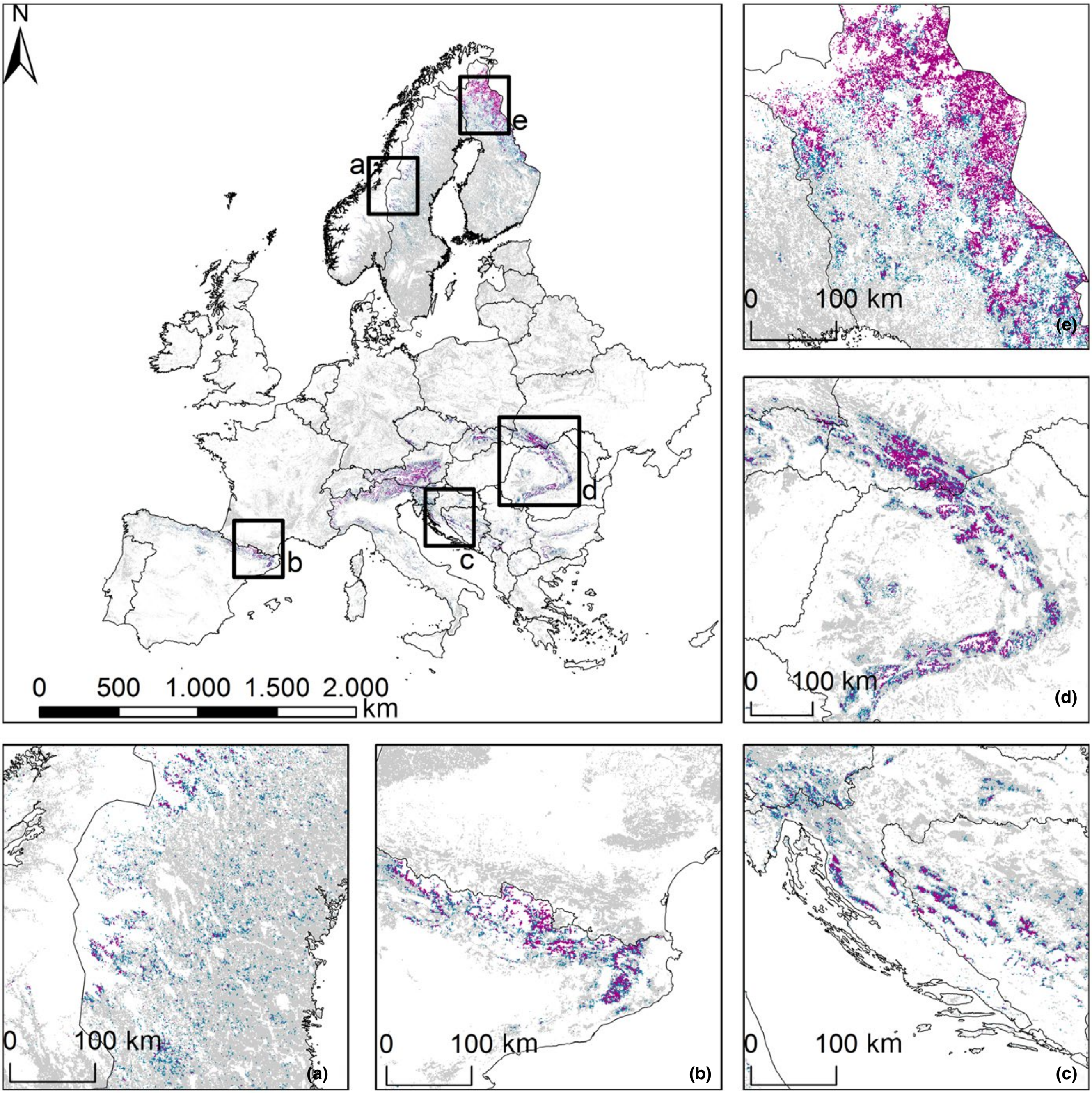

FIGURE 5 Areas with the highest likelihood of occurrence of primary forest in Europe at a 1 × 1 km resolution. The top-ranking 5% pixels were highlighted in purple and the 90–95th percentile in blue. Forests are reported in grey and follow Gallaun et al. (2010) [Colour figure can be viewed at wileyonlinelibrary.com]

the highest parts of the Pyrenees. Areas with low primary forests likelihood were the Atlantic region, the Britannic Archipelago, the Middle European lowlands, the Pannonian plain and the hemiboreal Baltic region. Areas with predicted and observed primary forest (Supporting Information Figure S5) matched in those regions where we had a high sampling size (northern Finland, Slovakian and Ukrainian Carpathians, Balkan mountains). On the contrary, our model predicted the occurrence of scattered and isolated primary forest patches in southern Finland, in the continental lowlands or in the western Mediterranean areas weakly. Only 38% of the area predicted to host primary forest was included in protected areas, of which only 5.6% was under strict protection (i.e., IUCN category I; Supporting Information Figure S6).

4 | DISCUSSION

Our study produced the most comprehensive spatially explicit dataset on known primary forests in Europe currently available. Known primary forests covered approximately 1.4 Mha in 32 European countries, which represent 0.25% of terrestrial Europe and 0.7% of Europe's forest area excluding Russia. This means that we managed to map about one-fifth of the 7.3 Mha of forest estimated to be "*undisturbed by man*" in Europe (FOREST EUROPE, 2015). We found a general increase in the number of primary forest patches from the west to the east and from the south to the north. Most of the primary forests in our dataset were located in Finland (0.9 Mha), in the Carpathians (0.16 Mha) and in the Balkans (0.08 Mha), although some important data gaps exist.

For many countries, we noted a mismatch between the total area of primary forest included in our map and the estimates reported in FOREST EUROPE (2015), possibly because these were based on the data not inherently designed for mapping primary forest, such as extrapolation from forest inventories (Italy, Norway) or remote sensing data not verified in the field (e.g., Romania, FOREST EUROPE, 2015). The area of primary forest we mapped for Finland is three times larger than previous estimates (FOREST EUROPE, 2015). It possibly depends on the fact that we considered as primary forests not only old-growth stands older than 160–200 years (as in FOREST EUROPE, 2015), but also those primary forests composed of a mosaic of successional phases occurring in the extreme north of Finland (Bernier et al., 2017; Kuuluvainen & Aakala, 2011; Potapov et al., 2017). On the contrary, the amount of primary forest area mapped for Sweden and the Carpathians is far lower than current estimates. For Sweden, we mapped only 0.03 Mha of primary forest, which represents <2% of the current estimation (2.4 Mha in FOREST EUROPE, 2015). Given that Sweden is expected to host the widest continuous stretches of primary forest of the European continent (Parviainen, 1999), this represents the most severe data gap of our dataset. Similarly, for the Carpathians, we mapped ca. 30% of the 0.44 Mha of primary forest currently estimated to exist (FOREST EUROPE, 2015). The data we aggregated for the Carpathians mostly derived from surveys coordinated within the framework of the UNEP—Carpathian Convention. Not only are these inventories still incomplete in countries such as Ukraine and Romania, but they also prioritize those forests having the highest naturalness levels. Therefore, a considerable share of forest of lower naturalness levels, but still qualifying as primary, may remain unmapped in the Carpathians (Kulakowski et al., 2017).

The low share of primary forest in Western Europe was expected considering the historically high population density, and long history of land use, especially in the Mediterranean (Jepsen et al., 2015). Species-rich Mediterranean forest types (i.e., FT8, FT9 and FT10) were particularly scarce in our map (Supporting Information Figures S2 and S3). Mediterranean forests show fundamentally different structural characteristics from temperate mesic forests, due to the high-drought stress Mediterranean forests experience during the summer and due to fire disturbance (Karavani et al., 2018). The role of wildfires in shaping the structure of Mediterranean primary forests is particularly complex as today most wildfires are human-induced (Ganteaume et al., 2013; Vacchiano, Garbarino, Lingua, & Motta, 2017). These conditions may hinder the development of structural features typically associated with old-growth stages, such as deadwood or large trees (Burrascano et al., 2013; Kulakowski et al., 2017). As these features are commonly used on the ground for identifying primary forests (at least in their late-successional stages), significant portions of Mediterranean primary forest may remain overlooked.

Primary forest disproportionately occurred in remote, scarcely populated areas, mostly in rugged mountain areas or at high latitudes (i.e., on land with low agricultural productivity or low profitability for forestry operations). This makes intuitively sense, as accessibility and the distance from markets or other centres of demand is one of the main drivers of land-use allocation. Indeed, in remote and unfavourable areas such as northern Fennoscandia and the Carpathians mountains, land-use history has been shorter and less intense than in the rest of Europe (Jepsen et al., 2015; Kulakowski et al., 2017), making the persistence of primary forests more likely. This finding is also consistent with previous work in Fennoscandia (Kuuluvainen & Aakala, 2011), as well as with the known bias in protected area distribution towards higher elevation and more remote locations (Joppa & Pfaff, 2009). Interestingly, accessibility and population density are also important spatial determinants for explaining the patterns of wood production and harvesting intensity in Europe (Levers et al., 2014; Verkerk et al., 2015). The correlation between primary forest and water availability probably reflects the same pattern, as a direct effect of water availability on the likelihood of finding patches of primary forests is unlikely and water availability is usually high in mountain and boreal regions. Finally, our model predicted an unexpectedly high likelihood of occurrence of primary forest in the rugged portions of the Pyrenees and the Alps. The Pyrenees and the Alps have a longer history of land use and higher historical rates of forest management intensity than other European mountain ranges, which our models could not account for.

Although difficult to map at high spatial resolution, historical land-use pressures played a key role in our model to explain present-day primary forest distribution. Primary forests, for instance, had a lower likelihood of occurring in those regions with higher historical wood demand (Figure 4), but only up to a threshold, after which the likelihood increased unexpectedly. We believe this relationship derives by the occurrence of several primary forest patches in some historical mining areas, where a historical high wood demand co-occurred with a high historical forest cover, such as the Upper Silesian Province (Poland). The historical variables we used, however, did not fully capture the role of historical events and contingencies. For instance, the occurrence of some primary forest patches may depend on the short distance from major historical political boundaries as in the case of the Bieszczady region (SE Poland) or the Rhodope mountains (between Greece and Bulgaria). The peripheral location of these regions and/or the lack of effective means for timber transportation left considerable areas of primary forest well into the 20th century. These areas could have followed a trajectory similar to other peripheral areas where primary forests were extensively cut in the last century if political upheavals, including the establishment of the Iron Curtain, had not occurred (Keeton et al., 2010). In addition to major historical events, peculiar local episodes could also explain the presence of some primary forest patches, such as Fonte Novello, a 50-ha old-growth stand in Gran Sasso National Park (central Italy), which is located at the boundary between two municipalities. Ownership of this forest remnant has been contented between the two municipalities since their formal establishment at the beginning of 19th century and remains unresolved as of today. This dispute coupled with the deep economic depression of this mountain area saved the stand from being exploited for timber and degradation until its recent "rediscovery" and protection. Other emblematic examples include primary forests that were set aside centuries ago as hunting grounds, such as in Białowieża (lowland Poland), Biogradska Gora National Park (Montenegro) or Central Bohemia (Czech Republic).

The result of an unprecedented international collaboration, our dataset should be considered as a necessary first step towards a more complete inventory. Important limitations include high variability in data quantity and quality across countries. Variability may derive from a different interpretation of FAO definition of primary forests. Although authoritative and widely accepted internationally, FAO definition is conceptual, rather than operational, which may result in inconsistencies in reporting among countries (Bernier et al., 2017). For many countries, no complete inventory exists, and data derive from the knowledge of local experts or from partial inventories with relatively narrow breadth, focussing on either forest inside (e.g., France, Italy and Finland) or outside protected areas (e.g., Norway) or specific regions (e.g., the Transcarpathian region of Ukraine, the French Pyrenees). In some countries, we found only incomplete data although extensive forestry statistics and databases are generally available for these countries. This was either because we did not manage to engage local researchers in helping us locate, extract and harmonize existing data (Latvia, Sweden) or because relevant data are kept strictly confidential by public authorities, possibly to avoid conflicts with private forest owners (e.g., Austria). While filling these knowledge gaps is a priority to achieve a more accurate description of primary forest distribution in Europe, the good-quality datasets we retrieved for neighbouring countries with similar ecological conditions (Norway and Finland in the case of Sweden, or Switzerland and Slovenia in the case of Austria) grant robustness to our statistical results. For other countries with abundant forest resources and presumably also a relatively high fraction of primary forest (e.g., many Balkan countries and Belarus), data were unavailable, at least in the international scientific literature or in digitized forms. In this case, we advocate a higher commitment from the international community to support local research institutions and NGOs in the collection or digitization of data on primary forests. Few data also exist for those countries with low forest cover (e.g., <10%) and in which significant areas of primary forest are unlikely to occur due to historic clearing or biophysical factors, such as the British Isles, Moldova or Cyprus.

Granting adequate protection to European primary forests should be a conservation priority (Mackey et al., 2015), especially given the recent concerns about commercial exploitation of old-growth forests in Eastern Europe (Chylarecki & Selva, 2016; Knorn et al., 2013). The majority (89%) of primary forest in our dataset is currently under some form of protection; nevertheless, its future protection remains uncertain. A high fraction of primary forest (54%) is currently outside strictly protected areas, and broad differences exist among European countries in the management restriction applied in other protected areas (Diaci, 1999; Parviainen, 2000; Verkerk, Zanchi, & Lindner, 2014). In some countries, some forest management activities (e.g., salvage logging) are allowed even in protected areas, representing a threat to primary forests (Thorn et al., 2018). Another concern is the small average size of primary forest patches. Even if protected, a small patch of forest may not be large enough to host the full range of ecological processes, and biodiversity may suffer from extinction debt (Peterken, 1996). When large patches of primary forest do not exist, maintaining existing patches in a large matrix of natural or seminatural forests should be the priority. This is necessary both to buffer the effects of direct and indirect anthropogenic disturbance on primary forests and because these patches could function as "strongholds" for the recovery and recolonization of many specialist species in the surrounding forest (Vandekerkhove et al., 2009). Our map of primary forest in Europe can therefore inform efforts aiming at preserving wilderness areas, in line with the requirements of the European Biodiversity Strategy and EU's Green Infrastructure Strategy. Given the current low share of primary forests, their restoration should be a priority throughout Europe (Navarro & Pereira, 2012; Schnitzler, 2014). Our map could be used to prioritize those regions and forest types for possible restoration efforts. For instance, our work highlighted areas, such as the most rugged parts of the Alps and the Pyrenees, where land-use pressure is relatively low and primary forests could potentially occur, thus suggesting that the opportunity costs of restoring primary forests and associated ecosystem processes and biodiversity in these areas may be lower than elsewhere.

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DATA ACCESSIBILITY

The data on primary forests here presented were collected within the F&CO-NET initiative and remain property of the institutions, organizations or person who created or collected them. The custodian of each dataset, that is person who owns or represents the contributed data, is listed in Supporting Information Table S3. F&CO-NET is available on request for disclosing data to individuals or groups of individuals for research or application purposes. Requests will be considered by the F&CO-NET coordinators (F.M. Sabatini, T. Kuemmerle) and data released after receiving the approval from the respective custodians. All derived data are available upon request from the corresponding author.

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BIOSKETCH

Francesco Maria Sabatini is interested in the processes and determinants underlying the distribution of plant biodiversity in forests. Most of his research has been on old-growth and virgin forests, regarded as reference systems for understanding baselines and processes related to natural disturbance regimes, forest dynamics, tree demography and carbon cycling.

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SUPPORTING INFORMATION

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

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