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Protection gaps and restoration opportunities for primary forests in Europe

Francesco M. Sabatini[1,2,3] | William S. Keeton[4] | Marcus Lindner[5] | Miroslav Svoboda[6] | Pieter J. Verkerk[7] | Jürgen Bauhus[8] | Helge Bruelheide[1,2] | Sabina Burrascano[9] | Nicolas Debaive[10] | Inês Duarte[11] | Matteo Garbarino[12] | Nikolaos Grigoriadis[13] | Fabio Lombardi[14] | Martin Mikoláš[6,15] | Peter Meyer[16] | Renzo Motta[12] | Gintautas Mozgeris[17] | Leónia Nunes[11,18] | Péter Ódor[19] | Momchil Panayotov[20] | Alejandro Ruete[21] | Bojan Simovski[22] | Jonas Stillhard[23] | Johan Svensson[24] | Jerzy Szwagrzyk[25] | Olli-Pekka Tikkanen[26] | Kris Vandekerkhove[27] | Roman Volosyanchuk[28] | Tomas Vrska[29] | Tzvetan Zlatanov[30] | Tobias Kuemmerle[3,31]

[1]Institut für Biologie, Martin-Luther-Universität Halle-Wittenberg, Halle, Germany

[2]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Germany

[3]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany

[4]Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA

[5]Resilience Programme, European Forest Institute, Bonn, Germany

[6]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Praha 6 – Suchdol, Czech Republic

[7]European Forest Institute, Joensuu, Finland

[8]Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany

[9]Department of Environmental Biology, Sapienza University of Rome, Rome, Italy

[10]Réserves Naturelles de France, Dijon Cedex, France

[11]Centre for Applied Ecology "Professor Baeta Neves" (CEABN), InBIO, School of Agriculture, University of Lisbon, Lisbon, Portugal

[12]Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, Grugliasco, Italy

[13]Forest Research Institute Thessaloniki, Thessaloniki, Greece

[14]Department of Agraria, Mediterranean University of Reggio Calabria – Feo Di Vito, Reggio Calabria, Italy

[15]PRALES, Rosina, Slovakia

[16]Northwest German Forest Research Institute, Göttingen, Germany

[17]Agriculture Academy, Institute of Forest Management and Wood Science, Vytautas Magnus University, Akademija, Lithuania

[18]CITAB, Centre of the Research and Technology of Agro-Environmental and Biological Science, University of Trás-os-Montes and Alto Douro, Vila Real, Portugal

[19]Centre for Ecological Research Institute of Ecology and Botany, Vácrátót, Hungary

[20]University of Forestry, Sofia, Bulgaria

[21]Greensway AB, Uppsala, Sweden

[22]Hans Em Faculty of Forest Sciences, Landscape Architecture and Environmental Engineering, Department of Botany and Dendrology, Ss. Cyril and Methodius University in Skopje, Skopje, North Macedonia

[23]Forest Resources and Management, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[24]Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

[25]Department of Forest Biodiversity, University of Agriculture in Krakow, Krakow, Poland

²⁶School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

²⁷Research Institute for Nature and Forest (INBO), Geraardsbergen, Belgium

²⁸NGO "Ecosphere" – Koshyts'ka, Uzhhorod, Ukraine

²⁹Silva Tarouca Research Institute, Brno, Czech Republic

³⁰Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria

³¹Integrative Research Institute on Transformation in Human-Environment Systems, Humboldt-Universität zu Berlin, Berlin, Germany

Correspondence

Francesco M. Sabatini, Institut für Biologie, Martin-Luther-Universität Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany.
Email: francesco.sabatini@botanik.uni-halle.de

Abstract

Aims: Primary forests are critical for forest biodiversity and provide key ecosystem services. In Europe, these forests are particularly scarce and it is unclear whether they are sufficiently protected. Here we aim to: (a) understand whether extant primary forests are representative of the range of naturally occurring forest types, (b) identify forest types which host enough primary forest under strict protection to meet conservation targets and (c) highlight areas where restoration is needed and feasible.

Location: Europe.

Methods: We combined a unique geodatabase of primary forests with maps of forest cover, potential natural vegetation, biogeographic regions and protected areas to quantify the proportion of extant primary forest across Europe's forest types and to identify gaps in protection. Using spatial predictions of primary forest locations to account for underreporting of primary forests, we then highlighted areas where restoration could complement protection.

Results: We found a substantial bias in primary forest distribution across forest types. Of the 54 forest types we assessed, six had no primary forest at all, and in two-thirds of forest types, less than 1% of forest was primary. Even if generally protected, only ten forest types had more than half of their primary forests strictly protected. Protecting all documented primary forests requires expanding the protected area networks by 1,132 km² (19,194 km² when including also predicted primary forests). Encouragingly, large areas of non-primary forest existed inside protected areas for most types, thus presenting restoration opportunities.

Main conclusion: Europe's primary forests are in a perilous state, as also acknowledged by EU's "Biodiversity Strategy for 2030." Yet, there are considerable opportunities for ensuring better protection and restoring primary forest structure, composition and functioning, at least partially. We advocate integrated policy reforms that explicitly account for the irreplaceable nature of primary forests and ramp up protection and restoration efforts alike.

KEYWORDS

biodiversity conservation, conservation priorities, gap analysis, old-growth forest, primary forest, protected areas, protection gap, restoration opportunities, strict protection, virgin forest

1 | INTRODUCTION

Primary forests continue to disappear worldwide (FAO, 2016; Mackey et al., 2015; Watson et al., 2016, 2018), even in regions where forests are expanding (Potapov et al., 2017; Song et al., 2018). Their loss is deeply concerning since primary forests are an irreplaceable part of our natural heritage (Watson et al., 2018) and are critical for conserving forest biodiversity (Di Marco, Ferrier, Harwood, Hoskins, & Watson, 2019; Dvořák et al., 2017; Gibson et al., 2011). Primary forests provide important ecosystem services, such as carbon storage and riparian functionality (Ford & Keeton, 2017; Warren, Keeton, Bechtold, & Kraft, 2019; Watson et al., 2018). And while they have

long been known to harbour high levels of biodiversity, particularly for certain taxa such as bryophytes, fungi, lichens and saproxylic beetles (Eckelt et al., 2018; Paillet et al., 2010; Watson et al., 2018), recent research has shown that primary forests frequently also have high functional trait diversity, which contributes to the resilience of ecosystem service outputs to global change (Messier, Puettmann, & Coates, 2013; Thom et al., 2019). Finally, where forest extent has declined or forests have been heavily altered from historic baselines, primary forests are also an important reference for guiding restoration and adapting to global change (Kuuluvainen, 2002; Parviainen, Bücking, Vandekerkhove, Schuck, & Päivinen, 2000).

Primary forests are naturally regenerated forests composed of native species, where signs of past human use are minimal and ecological processes, such as natural disturbances, operate dynamically and with little impairment by anthropogenic influences (Barton & Keeton, 2018; CBD, 2006; FAO, 2015). Globally, about one-third of all forests can be considered primary, but most are located in remote areas in the tropics, boreal zones or mountain regions (Potapov et al., 2017). By contrast, primary forests are scarce in the sub-tropical and temperate zones (Sabatini et al., 2018; Watson et al., 2016). In Europe, millennia of land use deeply transformed the forested landscapes (Kaplan, Krumhardt, & Zimmermann, 2009), so that very few forests remain with minimal signs of human use (<4% of forest area; FOREST EUROPE, 2015b). Yet, it is unclear whether these remnants are representative of the range of natural forest types found in Europe (Sabatini et al., 2018), and whether they are effectively protected.

Where primary forests still exist, ensuring that a sufficiently large area is adequately protected should be the first priority from a conservation perspective. Yet, there is a lack of consensus on how much primary forest should be protected for safeguarding biodiversity (Lõhmus, Kohv, Palo, & Viilma, 2004; Mair et al., 2018; Noss et al., 2012; Parviainen et al., 2000; Visconti et al., 2019). For instance, the Aichi target #11 of the Convention of Biological Diversity requires 17% of terrestrial land to be conserved in ecologically representative systems of protected areas (CBD, 2010). In its National Strategy on Biological Diversity, Germany committed to protecting at least 5% of forested areas in wilderness areas (Schumacher, Finck, Riecken, & Klein, 2018). Yet, most international agreements (CBD, 2010; European Commission, 1992; UN General Assembly, 2015) do not explicitly refer to primary forest, which adds uncertainty to conservation objectives (Chiarucci & Piovesan, 2019; Mackey et al., 2015; Watson et al., 2018). Only recently the EU commission released a new "Biodiversity Strategy for 2030," which emphasizes the need to define, map, monitor and strictly protect all of the EU's remaining primary and old-growth forests (European Commission, 2020). Until this strategy comes into force, however, many primary forests remain unprotected (Mikoláš et al., 2019; Sabatini et al., 2018), and it is unclear in which forest types such protection gaps are largest.

Where protection does exist, it should be sufficiently strict to avoid primary forest degradation. Many protected areas allow for human activities (e.g. salvage logging) that could jeopardize natural forest dynamics, such as successional recovery from natural disturbance and carryover of biological legacies (Mikoláš et al., 2019; Thorn et al., 2018). Such activities should thus be banned from primary forests, if the goal is to allow these forests to develop naturally. Identifying upgrading gaps (i.e. protected areas requiring an upgrade to strict protection) is therefore a second major priority to safeguard primary forests in the long-term.

Finally, given the overall very small area still covered by primary forest for most forest types, even protecting these areas entirely is likely insufficient for meeting biodiversity targets for many forest types (Keenelyside, Dudley, Cairns, Hall, & Stolton, 2012). Where the area of extant primary forest is too low, promoting the development of primary forest structure, composition and functioning in non-primary (e.g. secondary and managed forests) forests is crucial. Depending on the context and starting conditions (e.g. connectivity, presence of keystone species), restoration could happen either passively (e.g. setting aside forest and discontinuing forest management, salvage logging or disturbance suppression) or actively (e.g. removing non-native species, translocating species, restoring natural hydrological conditions or promoting the development of key structural elements, such as deadwood or veteran trees; Keenelyside et al., 2012; Mazziotta et al., 2016; Mikoláš et al., 2019; Schnitzler, 2014). Still, restoring conditions closer to those found in primary forests faces many challenges, not the least of which is the long timeframes involved. Where primary forests are scarce, lack of regeneration material may impede restoration of compositional diversity. Climate change adds uncertainty, as it is unclear where species may thrive in the future (Cernansky, 2018). Yet, it provides an additional argument for forest restoration, because increasing the structural and compositional diversity of forests improves their resistance and resilience to climate change effects (Barton & Keeton, 2018; Betts, Phalan, Frey, Rousseau, & Yang, 2018; Mair et al., 2018). Identifying where restoration gaps exist (i.e. areas where restoring primary forests is needed and feasible) is therefore a third conservation priority.

Building on a unique and comprehensive spatial database of documented primary forests in Europe (Sabatini et al., 2018), as well as on country-level statistics of primary forests (FOREST EUROPE, 2015b), here we address three questions:

1. Are remaining primary forests representative of Europe's biogeographic diversity and forest types?
2. Which forest types have a sufficient proportion of primary forest under strict protection and which forest types would meet different conservation targets?
3. Where would primary forest restoration efforts best complement protection to reach long-term conservation targets?

Compared to our previous work (Sabatini et al., 2018), which focused on understanding the spatial determinants underlying the current distribution of known primary forests, this study advances existing knowledge on primary forests by (a) systematically assessing their extent and distribution in relation to biogeographical regions

and forest types in Europe and (b) comprehensively characterizing and mapping different conservation gaps. By identifying protection and restoration gaps and priorities, in particular, we contribute to the scientific knowledge urgently needed for developing an integrated strategy for protecting and restoring forests with primary characteristics across Europe's landscapes, as called for in the framework of the new "EU Biodiversity Strategy for 2030" (European Commission, 2020).

2 | METHODS

2.1 | Input data

As acknowledged by the Convention of Biological Diversity, the term *"primary forest"* has a different connotation in Europe compared to the rest of the world. It refers to forests which have never been completely cleared, at least throughout historical times, even if traditional human disturbances (e.g. coppicing, burning, partial logging) may have occurred (CBD, 2006). In line with the Food and Agricultural Organization (FAO, 2015), here we consider a forest as *"primary"* where the signs of former human impacts, if any, are strongly blurred due to decades (at least 60–80 years) without forestry operations (Buchwald, 2005). We do not imply, therefore, that these forests were never cleared nor disturbed by humans.

We used a novel database of primary forests in Europe, excluding Russia (Sabatini et al., 2018). This map aggregates and harmonizes information derived from existing local-to-regional maps and datasets, scientific literature and original data from forest experts. In total, the map includes 1.4 Mha of primary forest across 32 European countries and represents a comprehensive, spatially explicit database on known primary forests in Europe (Sabatini et al., 2018).

To assess the distribution of Europe's total forested area, we used a high-resolution (25 m) map of forest cover (Kempeneers, Sedano, Seebach, Strobl, & San-Miguel-Ayanz, 2011), which we aggregated at 250-m resolution (pixel size = 6.25 ha) for computational reasons. Since this map does not cover some Eastern European countries (e.g. Ukraine, Belarus or Moldova), we integrated it with data on fractional tree cover (original resolution 30 m) from the Global Forest Watch (Hansen et al., 2013), which we also aggregated to a resolution of 250 m. Percentage forest (or tree) cover estimated using these two data sources had a good match in overlapping areas (i.e. Poland, Slovakia and Romania), with Pearson's r correlation estimated over 1,000 random points (with a 5 km minimum distance between points) of 0.87 ($p < .001$). For our analysis, we defined each 6.25 ha pixel as forest when forest\tree cover was >40%. This threshold discriminates between open and closed forests as defined by FAO (FAO, 2018).

We derived a map of forest types following a multi-step procedure. We started with the map of the potential natural vegetation of Europe (BfN, 2003), which reports potential zonal and azonal vegetation that would occur after a successional process undisturbed by humans. Next, we cross-linked the >700 legend classes from this

map to the 13 forest categories (plantations excluded) defined by the European Environmental Agency (EEA, 2006), as in Table S1. By aggregating classes belonging to the same category, we could then create a map with the potential distribution of forest categories in the absence of human disturbance. We then masked the map of potential forest categories with the forest-cover map to quantify the actual amount of forest area in each category (Figure S1). Disaggregating categories across Europe's biogeographical regions (BfN, 2003) yielded 54 forest types, defined as the combination between forest category and biogeographical region.

2.2 | Accounting for reporting gaps

To account for underreporting of primary forests data, we created a composite dataset complementing different data sources. For each country, we calculated the difference between the fraction of forests contained in the map of primary forests (Sabatini et al., 2018), and the country area estimates of forest undisturbed by man (FOREST EUROPE, 2015b). The latter data are based on national interpretations of forest undisturbed by man and typically derive from forest inventories or individual studies (FOREST EUROPE, 2015a). We considered this difference as an estimate of the amount of primary forest not yet mapped for each country (Table S2). We then assigned a corresponding fraction of forested area to primary forest, based on the likelihood that each 250 m grid cell contains primary forests.

To calculate this likelihood, we trained a spatially explicit boosted regression tree (BRT) model relating the presence of primary forests (response variable) to a set of 15 non-collinear (Pearson's $r < 0.7$) biophysical, socio-economic and historical land use predictors (Table S3). This model is conceptually equivalent to the one presented in Sabatini et al. (2018), but downscaled to a 250 m resolution. Since spatial clustering might lead to inaccurate models (Phillips et al., 2009), we rarefied primary forest presence points based on a 5×5-km grid. We selected 37,060 pseudo-absence points (i.e. ten times the number of presences after rarefaction), stratified to control for the unequal sampling intensity across different European countries or administrative regions. We set a learning rate of 0.02, a tree complexity of 5 and a bag fraction of 0.7. We used the *gbm. step* routine provided by the R *dismo* package (Hijmans, Phillips, Leathwick, & Elith, 2011) to determine the optimal number of trees ($n = 1,650$). We also reported the relative importance of each predictor, that is, the number of times that a variable was selected for splitting in the BRT model, weighted by the squared improvement to the model averaged over all trees (Elith et al., 2006) and produced partial dependency plots for the most important predictors.

2.3 | Representativeness of primary forests

To evaluate the representativeness of primary forest distribution along environmental gradients, we compared the probability–density distributions between the forested area of Europe, and the database

of documented primary forests (Sabatini et al., 2018), separately for each biogeographical region. For this analysis, we used only the database of documented primary forests (i.e. not the composite dataset outlined above). We considered five environmental variables: elevation (NASA, 2006), yearly solar radiation (NASA, 2006), growing degree days (>5°C) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), water availability (i.e. the ratio of actual over potential evapotranspiration, referred to as Priestley–Taylor alpha coefficient in Trabucco & Zomer, 2010) and suitability to agricultural crops (Zabel, Putzenlechner, & Mauser, 2014). We considered elevation as a proxy for forest accessibility. Yearly solar radiation provides a quantitative estimation of topography-related productivity at a given latitude. We preferred growing degree days over mean annual temperature since it better represents the growing conditions during the vegetative season. Similarly, we assumed the ratio of actual over potential evapotranspiration to provide a better representation of water availability compared to mean annual precipitation. Finally, we used suitability to agricultural crops to account for site productivity and land use competition.

To account for collinearity in the environmental data, we also compared the distribution of forested area in Europe to that of primary forest using a principal component analysis (PCA). After scaling each variable to zero mean and unit standard deviation, we ran a PCA of all the forested 250 m pixels of Europe. We then tested whether the density estimates of the distributions of forested area pixels and primary forest pixels in the PCA space originated from the same (multivariate) distribution. We estimated the probability-density functions in the PCA space using a kernel density estimation and then compared these between forested and primary forest pixels using a squared discrepancy measure. As this comparison test is non-parametric and asymptotically normal, it does not require any subjective decisions, nor the usual resampling techniques to compute *p*-values. We used the function *kde.test* in the R package *ks* (Duong, Goud, & Schauer, 2012).

To explore whether primary forests are representative of Europe's forest types, we first attributed each primary forest pixel to its respective forest type using the map of potential forest types described above. We did this because compositional data were only available for a subset of primary forests. This approach assumes, therefore, that all primary forests belong to their respective potential forest type. For each forest type, we then calculated: (a) the current extent of all forest, (b) the extent of primary forest and (c) the fraction of forest in primary conditions. We limited the analysis to forest types with a potential extent >1,000 km^2 and ran this comparison both using the primary forest database (documented primary forests only) and the composite dataset.

2.4 | Quantifying protection, upgrading and restoration gaps

Given the lack of consensus on how much primary forest should be conserved in Europe, we considered three alternative conservation targets: 17% (according to the Aichi target #11; CBD, 2010), 10% and 5% of forest area in primary state. We deemed there to be a protection

gap for a given forest type when insufficient amounts of primary forests were within protected areas to meet conservation targets, but only when additional primary forests for those forest types occurred outside protected areas. Similarly, we identified upgrading gaps for those forest types where primary forests are formally protected, but not yet included within strictly protected areas. We considered strict protection (= IUCN category I and II) to be the only protection level sufficient to ensure long-term conservation of primary forests, since in some European countries forest management (e.g. partial cutting, salvage logging) is allowed even in protected areas with lower protection level (e.g. Natura 2000 areas). Finally, we indicated as restoration gaps those situations when not enough primary forest exists, so that restoration is required to reach a conservation target.

To quantify these three conservation gaps, we calculated the share of primary forest under different protection levels for each forest type. We used spatial information on protected areas from the World Database on Protected Areas (UNEP-WCMC, & IUCN, 2019). We conservatively considered those protected areas where the IUCN category was not specified (e.g. Natura 2000 areas) as being protected, but not strictly. This yielded, for each forest type, the area and share of primary forest currently unprotected (protection gaps) or outside strictly protected areas (upgrading gaps). Similarly, we quantified the area and share of forested land that would have to undergo restoration to meet a given conservation target (restoration gaps) as the difference between a conservation area target and the current amount of primary forests for that forest type. For visualization purposes, we used treemap graphs (Tennekes, 2017), where we show the 17%, 10% or 5% forest area having the highest conservation status (two levels: primary, non-primary) and protection status (three levels: strict—IUCN protection category I and II, other—IUCN categories III-VI, and no protection) for each forest type. We ran this analysis both using our database of documented primary forests and the composite dataset, which accounts for underreporting of primary forest data.

The analyses based on documented primary forest alone or on the composite dataset are highly complementary. The former returns a more accurate representation of protection and upgrading gaps, but overestimates the amount of restoration gaps. The latter generates better estimates of restoration gaps, but quantifies protection and upgrading gaps less accurately due to the uncertain location of undocumented (=predicted) primary forests. Therefore, we presented the results of both analyses, but gave them different emphases depending on the specific conservation gap. For protection and upgrading gaps, we presented the results based on documented primary forest alone in the main text, and those based on the composite dataset in the supplementary material. For restoration gaps, we did the opposite.

2.5 | Mapping restoration opportunities

To pinpoint the most favourable areas where restoration could complement protection to reach primary forest conservation targets (17%, 10 or 5%), we mapped restoration opportunities. We selected
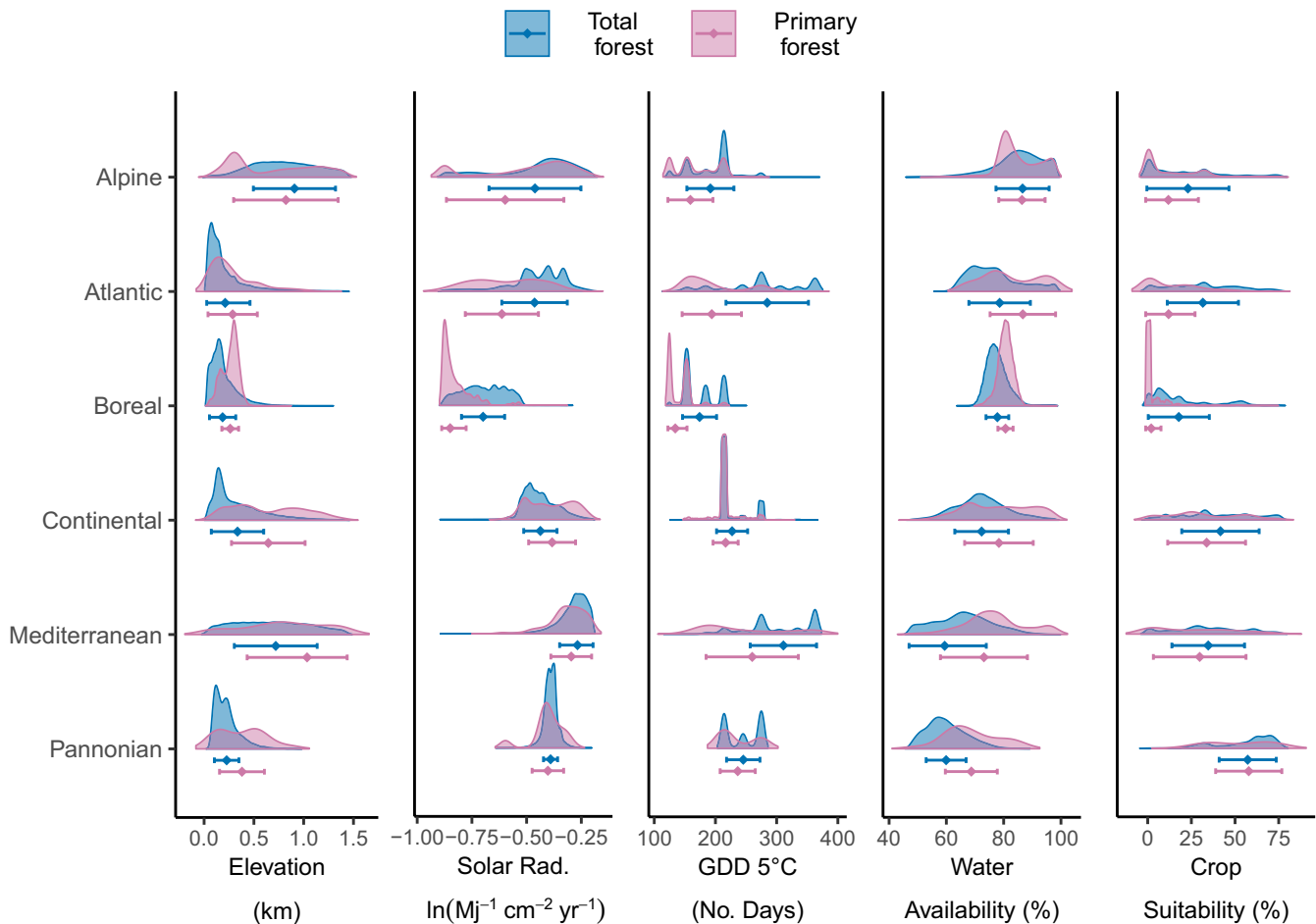
FIGURE 1 Distribution of total and primary forest cover along main environmental gradients. The y-axis represents the proportion of 250 m pixels covered with either forest (blue), or primary forest (pink), so that the areas under the curves are equivalent. We only considered those biogeographical regions with more than 10,000 km² of total forested area. Dots and horizontal bars, respectively, represent the mean and standard deviation of the distributions. Outliers (<2.5th and >97.5th percentiles) are not shown [Colour figure can be viewed at wileyonlinelibrary.com]

areas suitable for restoration by selecting forested areas with the highest likelihood to contain primary forests, based on the BRT model described above. Since our BRT model showed that socio-economic (i.e. accessibility, population density) and land use (i.e. agricultural suitability, wood increment) determinants were good predictors of primary forest location, we interpreted areas with higher likelihood of containing primary forest as areas having lower land use pressure and thus greater suitability for primary forest restoration. We prioritized forests in protected areas, because we assume restoration has lower opportunity costs and higher social acceptability there. We mapped restoration gaps separately for each forest type, again using both datasets (documented primary forests and composite). In the first case, the areas with the highest likelihood of containing primary forests were all considered as areas suitable for restoration. In the second case, these areas were split between additional (predicted) primary forest and forest suitable for restoration.

We visualized the output of these analyses in two ways. First, we built a choropleth showing the share of forested pixels in need of conservation action (i.e. protection, upgrading or restoration gaps) at the level of first- or second-order (depending on country size)

administrative regions in Europe (Global Administrative Areas, 2012). Second, we aggregated the results into hexagonal forest landscapes (ca. 6,000 km²) and reported the biggest conservation gap per landscape, separately for each forest type. We ranked gaps as follows: (a) unprotected primary forests (=protection gap), (b) primary forests occurring in protected areas of IUCN category III or higher (=upgrading gap), (c) areas favourable for restoration in protected areas (=restoration gap) and (d) areas favourable for restoration outside protected areas (=restoration + protection gap). These maps show neither primary, nor non-primary forests in strictly protected areas, as these areas do not require conservation actions.

3 | RESULTS

3.1 | Biogeographical bias in primary forest distribution

Primary forests encompassed remarkably well the variability in climate (solar radiation, growing degree days—GDD 5°, water

availability), topography (elevation) and soil productivity (agricultural suitability) occurring in Europe's biogeographical regions (Figure 1). However, there were some key differences between the distribution of primary forests and total forest cover. Primary forests were over-represented at high elevations (except for the Alpine region) and at the low end of the solar radiation gradient in the Alpine, Atlantic and Boreal biomes. They also occurred more often where yearly solar radiation is low, that is, where topographical conditions are relatively unfavourable, such as on steep and/or north-facing-slopes. Primary forests also occurred more frequently in colder conditions (low GDD), where water availability is higher (with the exception of the Alpine region), and on land less suitable for agriculture, especially in the Alpine, Atlantic and Boreal biomes.

The tendency towards high elevation, cold and wet conditions with low yearly solar radiation was also visible after accounting for collinearity between variables and comparing the distribution of primary and total forest in the multivariate environmental space defined by a principal component analysis (PCA; Figure 2). The two multivariate distributions were significantly ($z = 383,805$, $p < .001$) different according to a kernel density based on global two-sample comparison test (Duong et al., 2012) referring to the first four principal components (97.3% of variation explained). This difference was also significant when considering each biogeographical region separately (Figure S2).

We found a substantial geographic bias in the distribution of primary forests across forest types, both when using the composite dataset and our primary forest database only. The composite dataset contains information on 3.5 Mha of primary forest (1.4 Mha from Sabatini et al. (2018), and 2.1 Mha predicted). The model underlying the composite dataset had a relatively high cross-validated area under the curve (AUC, mean $\pm$ *SD* range 0.86 $\pm$ 0.007) and correlation between observed and predicted primary forest likelihood ($r_{cv} = 0.63 \pm 0.007$). After controlling for spatial sorting bias (Hijmans, 2012), AUC reduced to 0.65 and r_{cv} to 0.29. The most important explanatory variables were forest growing stock (relative influence 12.1%), population density (10.7%), forest cover in 1,850 (9.6%) and accessibility (8.3%). Specifically, the model stresses that primary forests are more likely to occur in less productive areas where current and historical anthropogenic pressure is low. Indeed, the likelihood of a pixel containing primary forest was higher where growing stock and human population density were lower, and forest cover in 1,850 AD was higher. The relationship with accessibility was more complex: primary forest likelihood increased for increasing travel time from major cities up to a certain threshold and then decreased abruptly (Figure S3).

Based on the composite dataset, for only one forest type (non-riverine alder, birch and aspen forest in the boreal biome), primary forest accounted for more than 17% of total forested area (Figure 3). Of the remaining forest types, only one had a proportion of primary forest >5%, and 13 forest types had a share of primary forest of 1%–5%. Another 33 forest types had between 0.01% and 1% of forest in primary state. For 13 of these, primary forest covered less than 1,000 ha. No remaining primary forests were documented, or predicted to exist, for the remaining six forest types, most of which
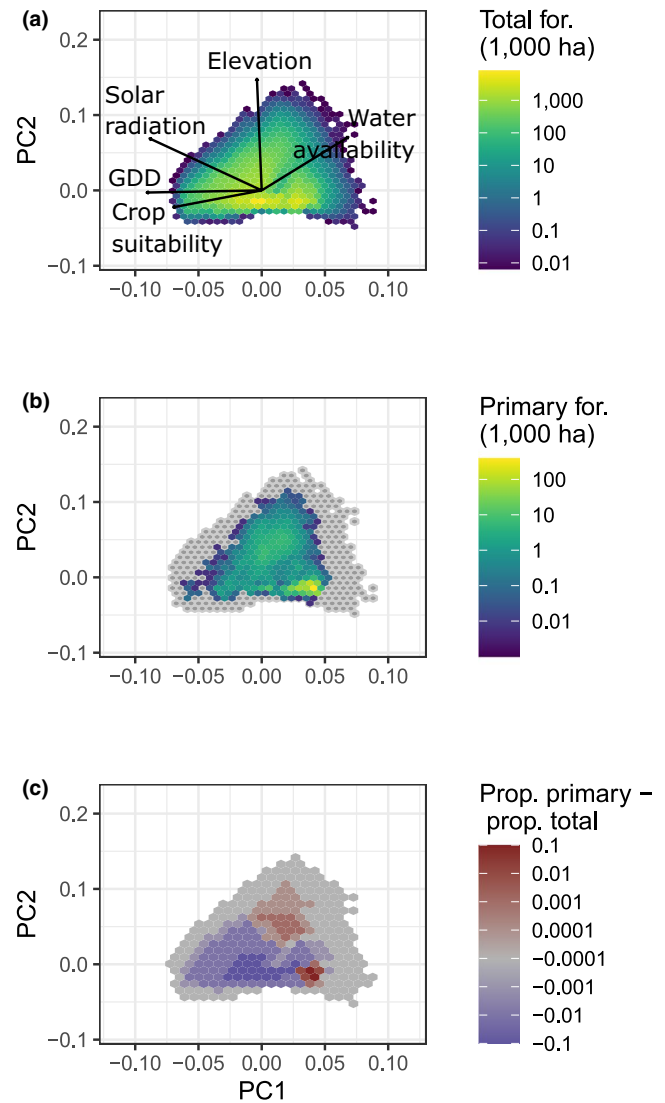

FIGURE 2 Distribution of (a) all European forests, (b) primary forests and (c) differences between the proportions of the two in the multidimensional environmental space. The graphs are based on a principal component analysis (PCA) based on elevation, growing degree days (GDD 5°C), water availability, yearly solar radiation and agricultural suitability. The first two principal components account for 47.4% and 26.7% of the overall variation, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

were located in the Atlantic and Alpine biomes (Figure 3). All these results changed only marginally when considering our original database of documented primary forests only (Figure S4). The number of forest types having a relatively high proportion of primary forests (1%–5%) decreased to seven, while those having little (0.01%–1%) primary forest increased to 37. No primary forest was found in nine forest types (Figure S4).

3.2 | Protection, upgrading and restoration gaps

When considering only our database of documented primary forests, protection gaps were not particularly widespread across Europe's
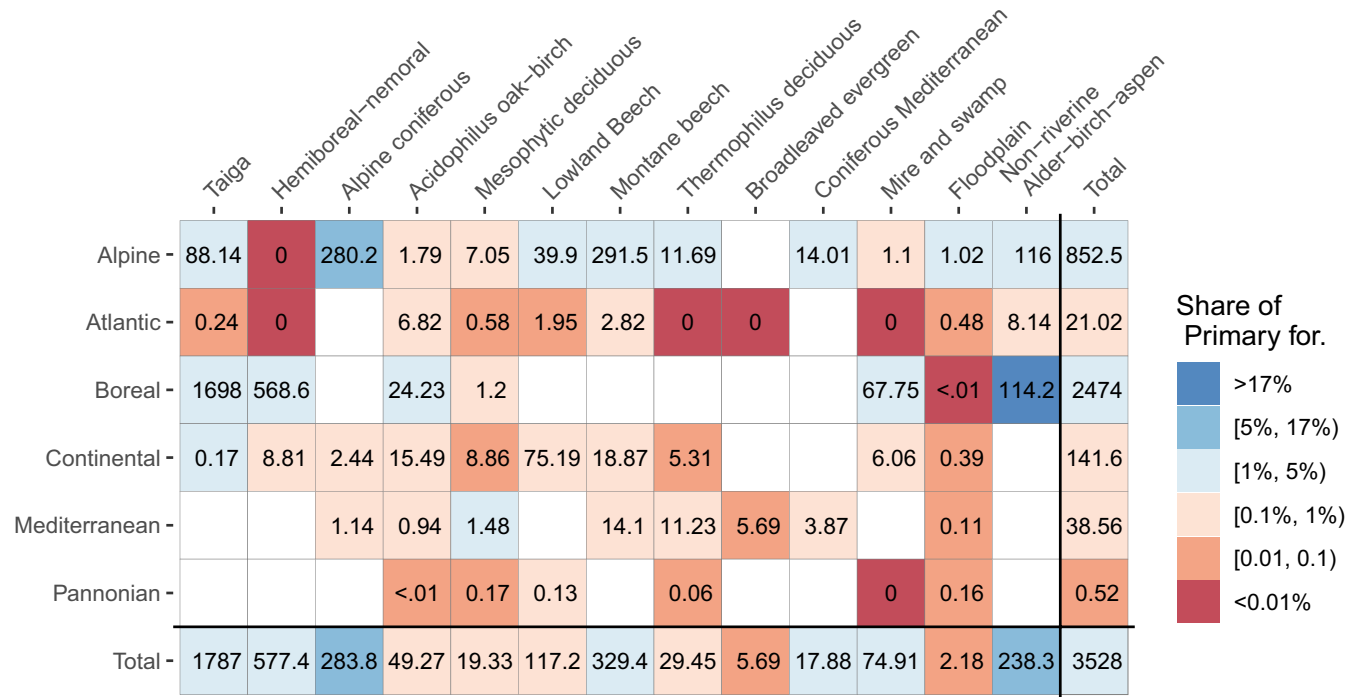
	Taiga	Hemiboreal–nemoral	Alpine coniferous	Acidophilus oak–birch	Mesophytic deciduous	Lowland Beech	Montane beech	Thermophilus deciduous	Broadleaved evergreen	Coniferous Mediterranean	Mire and swamp	Floodplain	Non-riverine Alder–birch–aspen	Total
Alpine	88.14	0	280.2	1.79	7.05	39.9	291.5	11.69		14.01	1.1	1.02	116	852.5
Atlantic	0.24	0		6.82	0.58	1.95	2.82	0	0		0	0.48	8.14	21.02
Boreal	1698	568.6		24.23	1.2					67.75	<.01	114.2		2474
Continental	0.17	8.81	2.44	15.49	8.86	75.19	18.87	5.31			6.06	0.39		141.6
Mediterranean			1.14	0.94	1.48		14.1	11.23	5.69	3.87		0.11		38.56
Pannonian				<.01	0.17	0.13		0.06			0	0.16		0.52
Total	1787	577.4	283.8	49.27	19.33	117.2	329.4	29.45	5.69	17.88	74.91	2.18	238.3	3528

Share of Primary for.

- >17%
- [5%, 17%)
- [1%, 5%)
- [0.1%, 1%)
- [0.01, 0.1)
- <0.01%

FIGURE 3 Share and amount of primary forests across forest types. Numbers indicate the absolute extent of primary forests in thousands of hectares as predicted when integrating data from Sabatini et al. (2018) and disaggregating data from FOREST EUROPE (2015b). White cells represent either non-existing forest types, or forest types having an amount of total forest cover below 1,000 km^2. Biogeographical regions follow BfN (2003), and forest categories follow EEA (2006) [Colour figure can be viewed at wileyonlinelibrary.com]

forest types. For only three forest types were there more than 80% of remaining primary forests located outside protected areas, while in an additional six forest types the proportion of unprotected primary forest was greater than 20% (Table S4; Figure S5). The situation was considerably less favourable for primary forest protection when basing the analysis on the composite dataset (Figure S6). In this case, large protection gaps (>80% of primary forest unprotected) occurred in about one fourth of the forest types we considered (n = 12) and in eight additional forest types, this proportion ranged between 50% and 80% (Figure S6). Protecting all documented primary forests in Europe would require expanding the current protected area networks by 1,132 km^2. This area increased to 19,194 km^2 when considering also undocumented (=predicted) primary forests (Table 1), although this figure should be seen as an upper bound due to the uncertain location of undocumented primary forests.

Upgrading gaps were very common, although for some countries the IUCN category of protected areas is not consistently specified (UNEP-WCMC, & IUCN, 2019). When considering documented primary forests only, there were 19 forest types where >80% of primary forest, albeit protected, was outside strict reserves of IUCN category I or II (Figure 4; Figure S5; Table S4). In an additional six and twelve forest types, this proportion was between 50%–80% and 20%–50%, respectively. More than half of the primary forest was under strict protection in only ten forest types. A total of 5,109 km^2 of documented primary forests qualified as in need of upgrading. When considering our composite dataset, the number of forest types with upgrading gaps exceeding 50% increased to eleven (Figure S6).

Based on our model, granting strict protection to all documented and predicted primary forests in Europe would require upgrading an additional 5,588 km^2 of protected areas (0.1% of Europe's land area, Table 1).

Meeting a 17% conservation target would require extensive restoration for most forest types (Figure 4). For most forest types, a high fraction of protected non-primary forests was coupled with smaller areas of primary forest (e.g. lowland, and montane beech forests in the Alpine biome). For some other forest types, however, there was neither enough primary forest, nor enough protected forest to fulfil a 17% target (e.g. the taiga forest in the Atlantic biome). This general situation neither changed for the least ambitious conservation target (i.e. 5%) nor when repeating the analysis using the composite dataset (Figure S7). Based on the composite dataset, an area approximately the size of Romania (226,236 km^2, 21.8% of Europe's forest area) should undergo restoration if the goal would be to ensure that 17% of Europe's forest approach primary, or close to primary conditions, at some point in the future (Table 1). Of this area, 28.6% is currently outside protected areas. Embracing conservation targets of 10% or 5% would decrease the required area to 107,440 and 30,331 km^2, respectively (Table 1).

3.3 | Restoration opportunities

We mapped the most favourable areas where restoration could complement protection to reach primary forest conservation targets

TABLE 1 Summary statistics for protection, upgrading and restoration gaps in Europe (excluding Russia). Only biogeographical regions hosting >10,000 km² of forest shown. These estimates are based on a composite dataset merging data from Sabatini et al. (2018) and country-level estimates from FOREST EUROPE (2015b)

	Alpine	Atlantic	Boreal	Continental	Mediterranean	Pannonian	Total
Land area							
km²	674,547	855,030	983,369	1,858,760	937,114	151,205	5,771,245
Forest area							
km²	226,962	126,722	662,233	570,294	150,355	18,441	1,770,381
%	33.65	14.82	67.34	30.68	16.04	12.20	30.68
Primary forest area							
km²	8,525	210	24,772	1,416	386	5	35,314
% of land area	1.26	0.02	2.52	0.08	0.04	0.00	0.61
% of forest area	3.76	0.17	3.74	0.25	0.26	0.03	1.99
Protection gaps[a]							
km²	3,304	146	14,855	642	247	1	19,194
% of land area	0.49	0.02	1.51	0.03	0.03	0.00	0.33
% of forest area	1.46	0.12	2.24	0.11	0.16	0.00	1.08
Upgrading gaps[a]							
km²	2,618	16	2,573	299	79	3	5,588
% of land area	0.39	0.00	0.26	0.02	0.01	0.00	0.10
% of forest area	1.15	0.01	0.39	0.05	0.05	0.02	0.32
Restoration gaps							
Target 17%							
km²	17,043	19,196	79,736	86,936	18,926	2,432	226,236
% of land area	2.5	2.2	8.1	4.7	2.0	1.6	3.9
% of forest area	7.5	15.1	12.0	15.2	12.6	13.2	12.8
% not protected	1.4	12.5	76.2	0.0	0.1	0.0	28.6
Target 10%							
km²	5,353	10,620	33,732	47,135	8,485	1,147	107,440
% of land area	0.8	1.2	3.4	2.5	0.9	0.8	1.9
% of forest area	2.4	8.4	5.1	8.3	5.6	6.2	6.1
% not protected	1.2	9.2	47.1	0.0	0.0	0.0	16.3
Target 5%							
km²	708	4,495	3,585	18,839	2,044	391	30,331
% of land area	0.1	0.5	0.4	1.0	0.2	0.3	0.5
% of forest area	0.3	3.5	0.5	3.3	1.4	2.1	1.7
% not protected	0.0	2.3	1.3	0.0	0.0	0.0	0.9

[a]Due to the uncertain location of undocumented (=predicted) primary forests, these figures should be taken with caution and seen as possible upper bounds, as we expect that a higher than random proportion of undocumented primary forests occur in protected areas.

(Figure S8). The map showed that, for many forest types, favourable areas were scattered throughout their respective biogeographical regions. This is the case, for instance, for the mesophytic deciduous forests in the continental region. For other forest types, we could instead identify key regions for restoration. For the acidophilous oak-birch forests of the Continental biome, for instance, priority restoration areas were clustered along the Ukraine–Belarus border, in Czech Republic, or in the western Cantabrian range. Similarly, for thermophilous deciduous forests, priority areas for restoration were widespread along the Apennines, as well as in the Spanish Pyrenees.
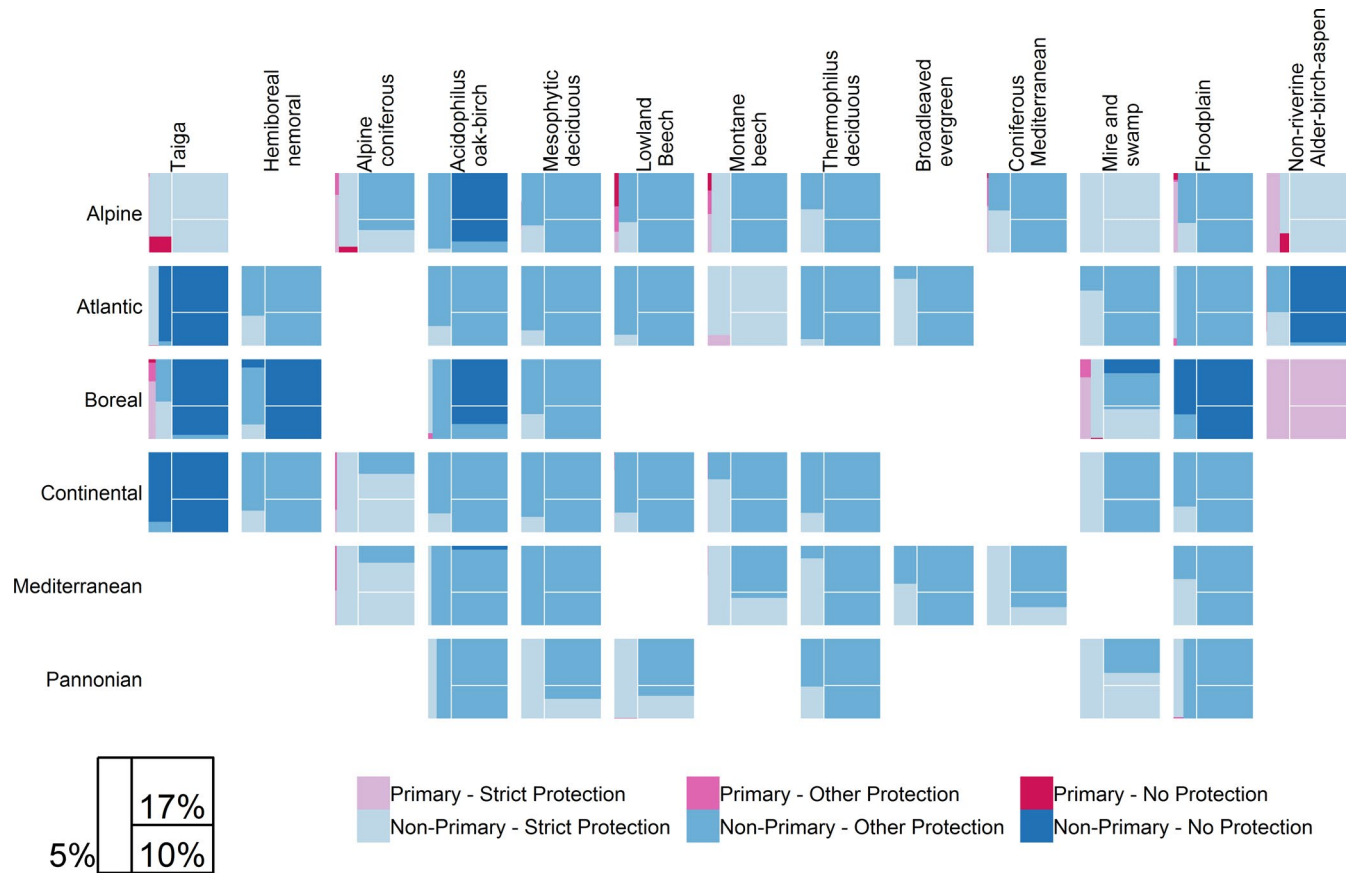
FIGURE 4 Distribution of forest area between primary and non-primary status, across protection levels and forest types. Only documented primary forest data from Sabatini et al. (2018) considered. Each square represents 17% of the area of each forest type. For each square, the size of the coloured rectangles is proportional to the area of forest in a given protection status (strict protection = IUCN I-II, other protection = IUCN III-VI, not protected) or conservation status (primary, non-primary). Squares are further divided in three rectangles, which cumulatively represent a 5% (left bar), 10% (left bar + bottom bar) and 17% (all square) of total forest. Rectangles are progressively filled considering forest area based on the following order: (a) strictly protected primary forest, (b) primary forest occurring in other protected areas, (c) unprotected primary forest, (d) strictly protected non-primary forest, (e) non-primary forest in other protected areas and (f) unprotected non-primary forest. In each rectangle, forest area in higher categories is only shown if the amount of forest area in lower categories does not reach the respective (5%, 10% or 17%) threshold. Only forest types with a total forest cover above 1,000 km^2 are shown [Colour figure can be viewed at wileyonlinelibrary.com]

For taiga forests, restoration opportunities were concentrated primarily in southern Finland (Figure S8).

When considering our composite dataset and all forest types jointly, restoration gaps dominated (Figure 5). Assuming a 17% target, a strong contrast emerged between the lowlands of Southern and Central Europe on the one hand, and Fennoscandia and the main European mountain ranges on the other. In Western Europe, for instance Great Britain, the Iberian Peninsula, Northern Italy and the lowland areas of France, Germany and Poland, little or no primary forest remains so that restoration gaps prevailed. In Fennoscandia and in the Alpine, Carpathian and Balkan mountain ranges, instead, not all primary forests were adequately protected, according to our analyses. These were either outside protected areas (e.g. Sweden or eastern Romania), or not strictly protected (e.g. Slovakia, Bosnia and Herzegovina, or Bulgaria) or their protection level was not consistently reported (e.g. Finland). Running the same analysis using our database of documented primary forests showed some marked shifts in conservation priorities, especially for data poor areas. In

Sweden, Belarus, Albania and the Alpine range, for instance, gaps in restoration replaced protection gaps (Figure S9). Differences were also substantial for the mountain regions of Southern Europe. Here, most documented primary forests were effectively protected (blue tones in Figure S9). Yet, these regions were also predicted to contain additional primary forests, which were either located outside strictly protected areas (see for instance the pink shades of the Italian Apennines in Figure 5) or were unprotected altogether (e.g. brown shades in Albania, Montenegro or southern Serbia).

4 | DISCUSSION

Primary forests are essential for biodiversity (Di Marco et al., 2019; Gibson et al., 2011; Watson et al., 2018), but are declining globally (Potapov et al., 2017; Watson et al., 2016). Yet, major uncertainties remain concerning the distribution of primary forests in Europe, their protection status, and for which areas and forest types restoration
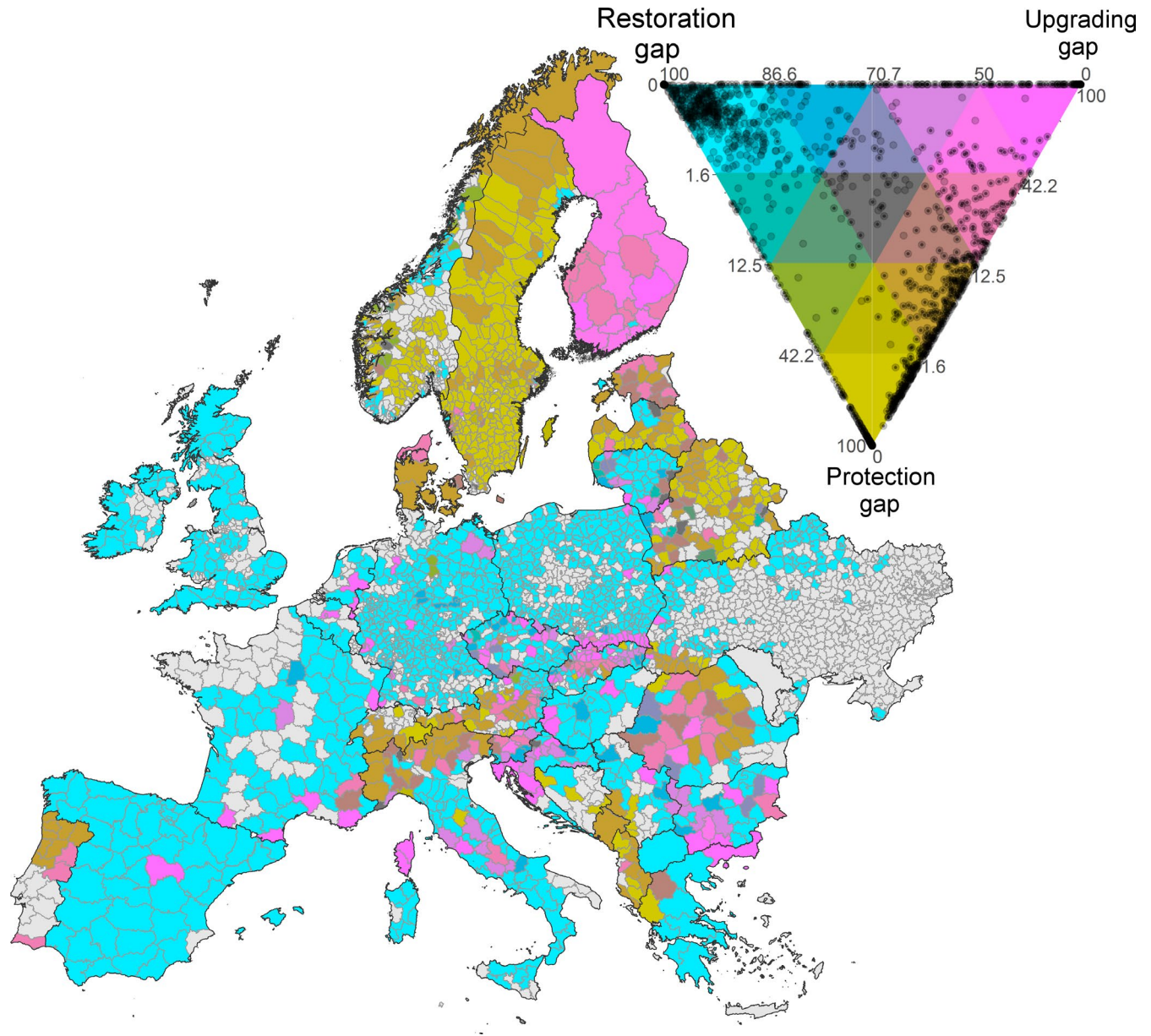
FIGURE 5 Distribution of conservation gaps regarding primary forests across European administrative units. For each unit, we highlighted the share of forested pixels classified as protection gaps (=unprotected primary forests), upgrading gaps (=protected primary forests outside strict reserves) and restoration gaps (=forests in areas favourable for restoration for forest types with less than 17% primary forest). All forest types are shown together. Only administrative units having more than 5 km^2 in any of the three gaps are shown. Each black dot in the triangular colour legend represents one administrative unit. Please note the axes of the triangular colour gradients are scaled differently to improve data visualization. This graph is based on a composite dataset integrating data from Sabatini et al. (2018) and FOREST EUROPE (2015a) [Colour figure can be viewed at wileyonlinelibrary.com]

efforts are most needed. By combining available data on the distribution of primary forests with a modelling approach, our study addresses these knowledge gaps, and pinpoints areas and forest types where restoration efforts would best complement protection to help reach long-term conservation targets.

Remaining primary forests are not evenly distributed across forest types and are only partially representative of the full range of environmental conditions in Europe. Almost three-quarters of all forest types (39 of 54) have no or less than 1% of primary forest remaining, which is likely insufficient to preserve the majority of

species associated with these forests (Lõhmus et al., 2004; Swanson et al., 2011). This is particularly critical in light of the fact that primary forests are crucial for the long-term persistence of many organismal groups and red-listed species in Europe, including insects (Eckelt et al., 2018), fungi and lichens (Ardelean, Keller, & Scheidegger, 2016; Moning & Müller, 2009).

Many primary forests in Europe are unprotected, which necessitates expansion of the current protected areas network. Protecting primary forests is more cost-effective than their restoration once they have been degraded (IUCN, 2016). Primary forests store more

carbon per hectare compared to logged, degraded or planted forests in ecologically comparable locations (Burrascano, Keeton, Sabatini, & Blasi, 2013; Watson et al., 2018) and often remain major net carbon sinks late into forest succession (Luyssaert et al., 2008). Granting them with adequate protection would therefore provide important climate benefits, besides enhancing biodiversity (Moomaw, Masino, & Faison, 2019). According to our analysis, designating 0.3% of Europe's land area (=1,132 km^2) as additional protected areas would be sufficient to safeguard all documented primary forest fragments, but protection would still be heavily biased towards the alpine and the boreal biomes. Similarly, urgent is the need to upgrade the protection level in about 5,109 km^2 of existing protected areas, where primary forest patches are not yet strictly protected. We consider these area estimates as lower bounds, since only about two fifths of Europe's primary forests have been mapped so far. When accounting for undocumented primary forests using a composite dataset based on modelling, the areas in need of protection and upgrade in protection increased to 19,194 and 5,600 km^2, respectively. Due to the uncertain location of undocumented (=predicted) primary forests, however, these figures should be seen as possible upper bounds, as we expect that a higher than random proportion of undocumented primary forests occur in protected areas. There is therefore the need to further improve our knowledge of the distribution of Europe's primary forests to reduce the uncertainty concerning these estimates.

Upgrading protected areas to ensure the long-term maintenance of primary forests requires a substantial change in conservation objectives, especially in the Natura 2000 network. The recently released "EU Biodiversity Strategy for 2030" explicitly mentions the need to effectively protect all remaining primary and old-growth forests in Europe and designate at least 10% of Europe's land under strict protection (European Commission, 2020). Although moving in the right direction, this strategy falls short by not ensuring that networks of strictly protected areas are fully representative of Europe's forest types. Even where the proportion of extant primary forests is low, existing protected areas contain large forest areas and thus provide important opportunities for restoration. Restoring existing forests towards their ecological potential represents a low-cost complement to other land-based solutions (e.g. afforestation, reforestation) to mitigate climate change, which promises to maximize biodiversity co-benefits (Griscom et al., 2017; Moomaw et al., 2019). We found that the areas with the most favourable socio-economic conditions for restoration coincide with those of low forest harvesting intensity and roundwood production (Levers et al., 2014; Verkerk et al., 2019). Prioritizing restoration in these areas would reduce the opportunity costs arising from taking forests out of timber production (Keenelyside et al., 2012). Particularly, favourable are those areas where harvesting intensity has been low in recent history (e.g. northern Fennoscandia, parts of the Carpathians, the Balkan region and the Apennines). For forest types mostly located in densely inhabited areas with high land use pressure, however, restoring the attributes of primary forests remains challenging. This is the case, for instance, for the lowland areas in the Atlantic or Mediterranean biomes. Yet, some of the areas highlighted by our model in these

regions are currently following a trajectory of land use de-intensification (Levers et al., 2018), such as the Trossachs in Scotland and the foothills of the southern Carpathians. In this context, abandonment of forest management in economically marginal areas may provide clear opportunities for restoring future primary forests at least in small forest patches. This would provide important benefits to biodiversity, since these restored patches might serve as refuges for rare or endangered species in these highly fragmented regions (Vandekerkhove et al., 2011).

Yet, restoring primary forests has many unsettled conceptual, economic and technical challenges (Bauhus, Puettmann, & Messier, 2009; Fahey et al., 2018; Keeton, Lorimer, Palik, & Doyon, 2019; Schnitzler, 2014) and requires long timeframes. Where the starting point is relatively natural forest, such as in long-established protected areas, passive rewilding approaches (Navarro & Pereira, 2012; Perino et al., 2019) may be sufficient to promote the redevelopment of the structure, function and composition of primary forest ecosystems (Thorn et al., 2018). Active restoration may instead prove more useful when the starting conditions are less favourable (e.g. young even-aged stands, non-adapted or non-native tree species composition, low genetic diversity; Keeton et al., 2019). Managing for old-growth characteristics, such as structural complexity, is an option, as it can accelerate stand development processes, establishment of late-successional biodiversity and ecosystem services such as carbon storage and flood resilience (Bauhus et al., 2009; Ford & Keeton, 2017; Keeton et al., 2019). Restoring natural disturbance regimes could be likewise desirable where primary forests, and the biodiversity therein, depend on infrequent, high-severity disturbance events, but this requires a careful consideration of possible drawbacks given the specific socio-ecological context (Kuuluvainen, 2002; Swanson et al., 2011). In all cases, increasing the diversity and complexity of Europe's forest ecosystems may reduce the future negative impacts of climate change (Barton & Keeton, 2018; Mair et al., 2018). Primary forests, for instance, have been shown to effectively buffer forest-floor summer temperatures compared to simplified forests (Frey et al., 2016), therefore mitigating climate change impacts for those species with the highest sensitivity to temperature increases (Betts et al., 2018).

Our work represents the first systematic analysis of the representativeness, conservation gaps and restoration opportunities of Europe's primary forests. Yet, some uncertainties need to be mentioned. First, the quality of the currently available data varies across countries (Sabatini et al., 2018). Nevertheless, no biogeographical region was systematically under-sampled, and the inclusion of additional country-level information to derive a composite dataset on primary forest (FOREST EUROPE, 2015b) further mitigates this potential bias. Yet, the location of predicted primary forests remains uncertain, so that figures based on the composite dataset should be taken with caution. Second, there is considerable inconsistency surrounding the application of IUCN protection categories for protected forest areas in Europe (Frank et al., 2007; Parviainen & Frank, 2003). At least for certain countries, some protected areas or alternative forms of protection (e.g. voluntary set-asides,

or certification schemes outside protected areas) may be granting adequate protection to primary forest patches, even without being categorized with the highest IUCN levels (Parviainen et al., 2000). This is, for instance, the case of Finland where many Natura 2000 areas, although not currently categorized as strict protected areas, may grant a sufficient level of protection to primary forests. If this is true, then the current upgrading gap of primary forests might change to restoration or protection gap in many areas in Finland (from pink to blue or brown in Figure 5). By contrast, in certain contexts even national parks may provide insufficient protection to primary forests, for instance where widespread salvage logging is allowed after insect, wind and fire disturbances (Mikoláš et al., 2019; Schickhofer & Schwarz, 2019). Finally, when prioritizing areas for restoration, our analysis neither explicitly accounted for opportunity costs, land tenure, productivity or rent, nor did we treat the uneven distribution of threatened species and biodiversity hotspots. Aligning restoration and conservation targets (e.g. habitat of threatened species), as well as other ecosystem services (e.g. timber provisioning) would be a useful follow-up undertaking for some biomes (Mönkkönen et al., 2014; Sabatini et al., 2019).

5 | CONCLUSIONS

Our work clearly highlights the overall perilous state of Europe's primary forests. The strong biogeographical bias we found highlights the urgent need for concerted, cross-national and multiscale conservation planning for Europe's forests. For instance, where primary forests are still relatively widespread, such as in parts of Eastern Europe, managers must be aware of the uniqueness of these forests in a broader biogeographical context. Recent reports of primary forest loss from these key areas (Mikoláš et al., 2017, 2019; Schickhofer & Schwarz, 2019) are, therefore, of greatest concern and require prompt and coordinated action. Likewise, even small regions could make important contributions to restoring missing primary forests for some forest types at the European scale. Systematic conservation planning (Margules & Pressey, 2000) provides an operational framework to prioritize areas for protection or restoration, with the goal of creating a functional and representative network of strictly protected primary forests, in synergy with other national to continental conservation initiatives (Perino et al., 2019; Schnitzler, 2014; Schumacher et al., 2018). The surge in demands for materials and bioenergy we experienced over recent years in Europe has translated into intensifying wood harvesting in many regions, including some that are crucial for primary forest conservation (Searchinger et al., 2018). This conjuncture further increases the urgency to protect and restore primary forests. The "decade of ecosystem restoration", as recently declared by the United Nations for 2021–2030, may provide momentum to set ambitious restoration goals. For example, this includes setting aside large areas where redevelopment towards forest landscapes composed of complex mosaics of seral habitats and late-successional stand structures will be encouraged, either actively or passively.

Primary forests are scarce and highly fragmented in Europe, which may engender vulnerability to anthropogenic stress and disturbance, impair species' and ecosystems' adaptive responses, and compromise species' capacity for refugial retreat (Angelstam et al., 2020; Mikoláš et al., 2019; Svensson, Andersson, Sandström, Mikusiński, & Jonsson, 2019), especially under the expected increase in disturbances under climate change (Seidl et al., 2017). Managed forests should play a key role in this regard. Retention forestry, for instance, integrates primary forest structures (e.g. deadwood, large trees, natural tree species composition) into managed forests, therefore increasing connectivity between forest reserves and contributing to preserve forest biodiversity across large scales (Gustafsson et al., 2012). Diversified forest management strategies efficiently balancing the trade-offs between timber production and biodiversity impacts are therefore a crucial complement to protection and restoration efforts in Europe (Eyvindson, Repo, & Mönkkönen, 2018; Mönkkönen et al., 2014; Sabatini et al., 2019).

The recently released "Biodiversity Strategy for 2030" has the merit of explicitly recognizing the irreplaceable nature of primary forests. Yet, this strategy should be coupled with an integrated forest policy reforms to prevent the continued loss of Europe's most valuable forests and in parallel ramp up both protection and restoration efforts for these forests. Only an effective management and governance of forest landscapes and resources, and a full recognition of the values and contributions of diverse states of forests can strategically ensure the maintenance and restoration of key ecosystem services and the fulfilment of human well-being in the long term (Chazdon, 2018).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13158.

DATA AVAILABILITY STATEMENT

The data on primary forests presented here remain the property of the institutions, organizations or persons who created or collected them. The custodian of each dataset (i.e. the person or institution owning or representing the contributed data) is listed in Sabatini et al., 2018 – https://doi.org/10.1111/ddi.12778. Data

are available from the corresponding author upon request for research or application purposes, subject to approval from the respective custodians. The composite dataset of primary forest is available at https://idata.idiv.de/ddm/Data/ShowData/1841 together with the maps of conservation gaps and restoration opportunities. All statistical code is available upon request from the corresponding author.

ORCID

Francesco M. Sabatini https://orcid.org/0000-0002-7202-7697
Marcus Lindner https://orcid.org/0000-0002-0770-003X
Pieter J. Verkerk https://orcid.org/0000-0001-5322-8007
Helge Bruelheide https://orcid.org/0000-0003-3135-0356
Matteo Garbarino https://orcid.org/0000-0002-9010-1731
Fabio Lombardi https://orcid.org/0000-0003-3517-5890
Peter Meyer https://orcid.org/0000-0003-4200-4993
Gintautas Mozgeris https://orcid.org/0000-0002-8480-6006
Leónia Nunes https://orcid.org/0000-0002-2617-0468
Péter Ódor https://orcid.org/0000-0003-1729-8897
Alejandro Ruete https://orcid.org/0000-0001-7681-2812
Bojan Simovski https://orcid.org/0000-0003-2905-1971
Johan Svensson https://orcid.org/0000-0002-0427-5699
Kris Vandekerkhove https://orcid.org/0000-0003-1954-692X
Tzvetan Zlatanov https://orcid.org/0000-0003-4205-3429
Tobias Kuemmerle https://orcid.org/0000-0002-9775-142X

REFERENCES

Angelstam, P., Manton, M., Green, M., Jonsson, B.-G., Mikusiński, G., Svensson, J., & Sabatini, F.M. (2020). Sweden does not meet agreed national and international forest biodiversity targets: A call for adaptive landscape planning. *Landscape and Urban Planning*, 202, 103838. https://doi.org/10.1016/j.landurbplan.2020.103838

Ardelean, I. V., Keller, C., & Scheidegger, C. (2016). Effects of management on lichen species richness, ecological traits and community structure in the Rodnei Mountains National Park (Romania). *PLoS ONE*, 10(12), e0145808. https://doi.org/10.1371/journal.pone.0145808

Barton, A. M., & Keeton, W. S. (Eds.). (2018). *Ecology and recovery of eastern old-growth forests*, Washington, DC: Island Press.

Bauhus, J., Puettmann, K., & Messier, C. (2009). Silviculture for old-growth attributes. *Forest Ecology and Management*, 258(4), 525–537. https://doi.org/10.1016/j.foreco.2009.01.053

Betts, M. G., Phalan, B., Frey, S. J., Rousseau, J. S., & Yang, Z. (2018). Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity and Distributions*, 24(4), 439–447. https://doi.org/10.1111/ddi.12688

BfN. (2003). *Map of natural vegetation of Europe*. Deutschland: Bundesamt fur Naturschutz. Retrieved from https://www.eea.europa.eu/data-andmaps/data/biogeographical-regions-europe-3

Buchwald, E. (2005). A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation. In *Proceedings: Third expert meeting on harmonizing forest-related definitions for use by various stakeholders* Rome, 17-19 January 2005: Food and Agriculture Organization of the United Nations.

Burrascano, S., Keeton, W. S., Sabatini, F. M., & Blasi, C. (2013). Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *Forest Ecology and Management*, 291, 458–479. https://doi.org/10.1016/j.foreco.2012.11.020

CBD. (2006). Indicative definitions taken from the Report of the ad hoc technical expert group on forest biological diversity. https://www.cbd.int/forest/definitions.shtml

CBD Secretariat. (2010). Strategic plan for biodiversity 2011–2020 including Aichi Targets. Convention on Biological Diversity. COP 10 Decision X/2.

Cernansky, R. (2018). How to plant a trillion trees. *Nature*, 560(7720), 542–545.

Chazdon, R. L. (2018). Protecting intact forests requires holistic approaches. *Nature Ecology & Evolution*, 2(6), 915. https://doi.org/10.1038/s41559-018-0546-y

Chiarucci, A., & Piovesan, G. (2019). Need for a global map of forest naturalness for a sustainable future. *Conservation Biology*.34(2), 368–372.

Di Marco, M., Ferrier, S., Harwood, T. D., Hoskins, A. J., & Watson, J. E. (2019). Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature*, 573(7775), 582–585.

Duong, T., Goud, B., & Schauer, K. (2012). Closed-form density-based framework for automatic detection of cellular morphology changes. *Proceedings of the National Academy of Sciences of the United States of America*, 109(22), 8382–8387.

Dvořák, D., Vašutová, M., Hofmeister, J., Beran, M., Hošek, J., Běťák, J., … Deckerová, H. (2017). Macrofungal diversity patterns in central European forests affirm the key importance of old-growth forests. *Fungal Ecology*, 27, 145–154.

Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., … Kadej, M. (2018). "Primeval forest relict beetles" of Central Europe: A set of 168 umbrella species for the protection of primeval forest remnants. *Journal of Insect Conservation*, 22(1), 15–28.

EEA. (2006). *European forest types. Categories and types for sustainable forest management reporting and policy*. Copenhagen. Retrieved from https://www.eea.europa.eu/publications/technical_report_2006_9

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

European Commission. (1992). *Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora*. Retrieved from https://eur-lex.europa.eu/eli/dir/1992/43/oj

European Commission. (2020) Biodiversity Strategy for 2030 Bringing nature back into our lives.

Eyvindson, K., Repo, A., & Mönkkönen, M. (2018). Mitigating forest biodiversity and ecosystem service losses in the era of bio-based economy. *Forest Policy and Economics*, 92, 119–127.

Fahey, R. T., Alveshere, B. C., Burton, J. I., D'Amato, A. W., Dickinson, Y. L., Keeton, W. S., … Puettmann, K. J. (2018). Shifting conceptions of complexity in forest management and silviculture. *Forest Ecology and Management*, 421, 59–71.

FAO. (2015). *Global Forest Resources Assessment 2015. Terms and definitions*. Rome, Italy: FAO.

FAO. (2016). *Global Forest Resources Assessment 2015. How are the world's forest changing?* Rome, Italy. Retrieved from http://www.fao.org/3/a-i4793e.pdf

FAO. (2018). *Forest Resource Assessment 2020 Guidelines and Specifications. v1.0*. Rome, Italy. Retrieved from http://www.fao.org/3/I8699EN/i8699en.pdf

Ford, S. E., & Keeton, W. S. (2017). Enhanced carbon storage through management for old-growth characteristics in northern hardwood-conifer forests. *Ecosphere*, 8(4), e01721.

FOREST EUROPE. (2015a). Quantitative Indicators Country reports 2015. Retrieved from https://foresteurope.org/state-europes-forests-2015-report/#1476295965372-d3bb1dd0-e9a0

FOREST EUROPE. (2015b). *State of Europe's Forests 2015*. Madrid. Retrieved from https://www.foresteurope.org/docs/fullsoef2015.pdf

Frank, G., Parviainen, J., Vandekerhove, K., Latham, J., Schuck, A., & Little, D. (2007). *COST Action E27. Protected Forest Areas in Europe-analysis*

and harmonisation (PROFOR): results, conclusions and recommendations, Vienna: Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW).

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, 2(4), e1501392. https://doi.org/10.1126/sciadv.1501392

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., ... Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369), 378. https://doi.org/10.1038/nature10425

Global Administrative Areas. (2012). *GADM database of global administrative areas*. Global Administrative Areas. Retrieved from https://gadm.org/

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., ... Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences of the United States of America*, 114(44), 11645–11650. https://doi.org/10.1073/pnas.1710465114

Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., ... Franklin, J. F. (2012). Retention forestry to maintain multifunctional forests: A world perspective. *BioScience*, 62(7), 633–645. https://doi.org/10.1525/bio.2012.62.7.6

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853. https://doi.org/10.1126/science.1244693

Hijmans, R. J. (2012). Cross-validation of species distribution models: Removing spatial sorting bias and calibration with a null model. *Ecology*, 93(3), 679–688. https://doi.org/10.1890/11-0826.1

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2011). Package 'dismo'. Retrieved from http://cran.r-project.org/web/packages/dismo/index.html

IUCN. (2016). Protection of primary forests, including intact forest landscapes. In *IUCN resolutions, recommendations and other decisions*, (pp. 108–109). Gland, Switzerland: International Union for Conservation of Nature and Natural Resources. https://portals.iucn.org/library/sites/library/files/documents/IUCN-WCC-6th-005.pdf

Kaplan, J. O., Krumhardt, K. M., & Zimmermann, N. (2009). The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*, 28(27–28), 3016–3034. https://doi.org/10.1016/j.quascirev.2009.09.028

Keenelyside, K., Dudley, N., Cairns, S., Hall, C., & Stolton, S. (2012). *Ecological restoration for protected areas: Principles, guidelines and best practices*, (Vol. 18). Gland, Switzerland: IUCN. https://www.iucn.org/content/ecological-restoration-protected-areas-principles-guidelines-and-best-practices

Keeton, W. S., Lorimer, C., Palik, B., & Doyon, F. (2019). Silviculture for old-growth in the context of global change. In A. Barton & W. S. Keeton (Eds.), *Ecology and recovery of eastern old-growth forests* (pp. 340). Washington, DC: Island Press.

Kempeneers, P., Sedano, F., Seebach, L., Strobl, P., & San-Miguel-Ayanz, J. (2011). Data fusion of different spatial resolution remote sensing images applied to forest-type mapping. *IEEE Transactions on Geoscience and Remote Sensing*, 49(12), 4977–4986. https://doi.org/10.1109/TGRS.2011.2158548

Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica*, 36(1), 97–125. https://doi.org/10.14214/sf.552

Levers, C., Müller, D., Erb, K., Haberl, H., Jepsen, M. R., Metzger, M. J., ... Kuemmerle, T. (2018). Archetypical patterns and trajectories of land systems in Europe. *Regional Environmental Change*, 18(3), 715–732. https://doi.org/10.1007/s10113-015-0907-x

Levers, C., Verkerk, P. J., Müller, D., Verburg, P. H., Butsic, V., Leitão, P. J., ... Kuemmerle, T. (2014). Drivers of forest harvesting intensity patterns in Europe. *Forest Ecology and Management*, 315, 160–172. https://doi.org/10.1016/j.foreco.2013.12.030

Lõhmus, A., Kohv, K., Palo, A., & Viilma, K. (2004). Loss of old-growth, and the minimum need for strictly protected Forests in Estonia. *Ecological Bulletin*, 51, 401–411.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., ... Grace, J. (2008). Old-growth forests as global carbon sinks. *Nature*, 455(7210), 213–215. https://doi.org/10.1038/nature07276

Mackey, B., DellaSala, D. A., Kormos, C., Lindenmayer, D., Kumpel, N., Zimmerman, B., ... Watson, J. E. M. (2015). Policy options for the world's primary forests in multilateral environmental agreements. *Conservation Letters*, 8(2), 139–147. https://doi.org/10.1111/conl.12120

Mair, L., Jönsson, M., Räty, M., Bärring, L., Strandberg, G., Lämås, T., & Snäll, T. (2018). Land use changes could modify future negative effects of climate change on old-growth forest indicator species. *Diversity and Distributions*, 24(10), 1416–1425. https://doi.org/10.1111/ddi.12771

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, 405(6783), 243–253.

Mazziotta, A., Heilmann-Clausen, J., Bruun, H. H., Fritz, Ö., Aude, E., & Tøttrup, A. P. (2016). Restoring hydrology and old-growth structures in a former production forest: Modelling the long-term effects on biodiversity. *Forest Ecology and Management*, 381, 125–133. https://doi.org/10.1016/j.foreco.2016.09.028

Messier, C., Puettmann, K., & Coates, D. (2013). *Managing forests as complex adaptive systems: Building resilience to the challenge of global change*. New York, NY: Routledge.

Mikoláš, M., Tejkal, M., Kuemmerle, T., Griffiths, P., Svoboda, M., Hlásny, T., ... Morrissey, R. C. (2017). Forest management impacts on capercaillie (*Tetrao urogallus*) habitat distribution and connectivity in the Carpathians. *Landscape Ecology*, 32(1), 163–179. https://doi.org/10.1007/s10980-016-0433-3

Mikoláš, M., Ujházy, K., Jasík, M., Wiezik, M., Gallay, I., Polák, P., ... Keeton, W. S. (2019). Primary forest distribution and representation in a Central European landscape: Results of a large-scale field-based census. *Forest Ecology and Management*, 449, 117466. https://doi.org/10.1016/j.foreco.2019.117466

Moning, C., & Müller, J. (2009). Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. *Ecological Indicators*, 9(5), 922–932. https://doi.org/10.1016/j.ecolind.2008.11.002

Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., ... Tikkanen, O.-P. (2014). Spatially dynamic forest management to sustain biodiversity and economic returns. *Journal of Environmental Management*, 134, 80–89. https://doi.org/10.1016/j.jenvman.2013.12.021

Moomaw, W. R., Masino, S. A., & Faison, E. K. (2019). Intact forests in the United States: Proforestation mitigates climate change and serves the greatest good. *Frontiers in Forests and Global Change*, 2, 27. https://doi.org/10.3389/ffgc.2019.00027

NASA. (2006). Shuttle Radar Topography Mission. Retrieved 01.09.16.

Navarro, L. M., & Pereira, H. M. (2012). Rewilding abandoned landscapes in Europe. *Ecosystems*, 15(6), 900–912. https://doi.org/10.1007/s10021-012-9558-7

Noss, R. F., Dobson, A. P., Baldwin, R., Beier, P., Davis, C. R., Dellasala, D. A., ... Tabor, G. (2012). Bolder thinking for conservation. *Conservation Biology*, 26(1), 1–4. https://doi.org/10.1111/j.1523-1739.2011.01738.x

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-römermann, M., ... Virtanen, R. (2010). Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology*, 24(1), 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x

Parviainen, J., Bücking, W., Vandekerkhove, K., Schuck, A., & Päivinen, R. (2000). Strict forest reserves in Europe: Efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). *Forestry*, 73(2), 107–118. https://doi.org/10.1093/forestry/73.2.107

Parviainen, J., & Frank, G. (2003). Protected forests in Europe approaches-harmonising the definitions for international comparison and forest policy making. *Journal of Environmental Management*, 67(1), 27–36. https://doi.org/10.1016/S0301-4797(02)00185-8

Perino, A., Pereira, H. M., Navarro, L. M., Fernández, N., Bullock, J. M., Ceaușu, S., ... Wheeler, H. C. (2019). Rewilding complex ecosystems. *Science*, 364(6438), eaav5570. https://doi.org/10.1126/science.aav5570

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, 19(1), 181–197. https://doi.org/10.1890/07-2153.1

Potapov, P., Hansen, M. C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., ... Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances*, 3(1), e1600821. https://doi.org/10.1126/sciadv.1600821

Sabatini, F. M., Burrascano, S., Keeton, W. S., Levers, C., Lindner, M., Pötzschner, F., ... Kuemmerle, T. (2018). Where are Europe's last primary forests? *Diversity and Distributions*, 24(10), 1426–1439. https://doi.org/10.1111/ddi.12778

Sabatini, F. M., de Andrade, R. B., Paillet, Y., Ódor, P., Bouget, C., Campagnaro, T., ... Burrascano, S. (2019). Trade-offs between carbon stocks and biodiversity in European temperate forests. *Global Change Biology*, 25(2), 536–548. https://doi.org/10.1111/gcb.14503

Schickhofer, M., & Schwarz, U. (2019). *Inventory of Potential Primary and Old-Growth Forest Areas in Romania (PRIMOFARO). Identifying the largest intact forests in the temperate zone of the European Union*. Vienna, Austria: EURONATUR. https://www.euronatur.org/fileadmin/docs/Urwald-Kampagne_Rumaenien/PRIMOFARO_24092019_layouted.pdf

Schnitzler, A. (2014). Towards a new European wilderness: Embracing unmanaged forest growth and the decolonisation of nature. *Landscape and Urban Planning*, 126, 74–80. https://doi.org/10.1016/j.landurbplan.2014.02.011

Schumacher, H., Finck, P., Riecken, U., & Klein, M. (2018). More wilderness for Germany: Implementing an important objective of Germany's National Strategy on Biological Diversity. *Journal for Nature Conservation*, 42, 45–52. https://doi.org/10.1016/j.jnc.2018.01.002

Searchinger, T. D., Beringer, T., Holtsmark, B., Kammen, D. M., Lambin, E. F., Lucht, W., ... van Ypersele, J.-P. (2018). Europe's renewable energy directive poised to harm global forests. *Nature Communications*, 9(1), 3741. https://doi.org/10.1038/s41467-018-06175-4

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., ... Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402. https://doi.org/10.1038/nclimate3303

Song, X.-P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F., & Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature*, 560(7720), 639–643. https://doi.org/10.1038/s41586-018-0411-9

Svensson, J., Andersson, J., Sandström, P., Mikusiński, G., & Jonsson, B. G. (2019). Landscape trajectory of natural boreal forest loss as an impediment to green infrastructure. *Conservation Biology*, 33(1), 152–163. https://doi.org/10.1111/cobi.13148

Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., ... Swanson, F. J. (2011). The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, 9(2), 117–125. https://doi.org/10.1890/090157

Tennekes, M. (2017). treemap: Treemap Visualization. R package version 2.4-2. Retrieved from https://CRAN.R-project.org/package=treemap

Thom, D., Golivets, M., Edling, L., Meigs, G. W., Gourevitch, J. D., Sonter, L. J., ... Keeton, W. S. (2019). The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America. *Global Change Biology*. https://doi.org/10.1111/gcb.14656

Thorn, S., Bässler, C., Brandl, R., Burton, P. J., Cahall, R., Campbell, J. L., ... Müller, J. (2018). Impacts of salvage logging on biodiversity: A meta-analysis. *Journal of Applied Ecology*, 55(1), 279–289. https://doi.org/10.1111/1365-2664.12945

Trabucco, A., & Zomer, R. J. (2010). *Global Soil Water Balance Geospatial Database. CGIAR Consortium for Spatial Information*.

UN General Assembly. (2015). *Transforming our world: The 2030 Agenda for Sustainable Development*, 21 October 2015, A/RES/70/1. Retrieved from https://www.refworld.org/docid/57b6e3e44.html

UNEP-WCMC, & IUCN. (2019). Protected Planet: The World Database on Protected Areas (WDPA). Retrieved from www.protectedplanet.net

Vandekerkhove, K., De Keersmaeker, L., Walleyn, R., Köhler, F., Crevecoeur, L., Govaere, L., ... Verheyen, K. (2011). Reappearance of old-growth elements in lowland woodlands in Northern Belgium: Do the associated species follow? *Silva Fennica*, 45(5), 909–935. https://doi.org/10.14214/sf.78

Verkerk, P. J., Fitzgerald, J. B., Datta, P., Dees, M., Hengeveld, G. M., Lindner, M., & Zudin, S. (2019). Spatial distribution of the potential forest biomass availability in Europe. *Forest Ecosystems*, 6(1), 5. https://doi.org/10.1186/s40663-019-0163-5

Visconti, P., Butchart, S. H. M., Brooks, T. M., Langhammer, P. F., Marnewick, D., Vergara, S., ... Watson, J. E. M. (2019). Protected area targets post-2020. *Science*, 364(6437), 239–241. https://doi.org/10.1126/science.aav6886

Warren, D. R., Keeton, W. S., Bechtold, H. A., & Kraft, C. E. (2019). Stream ecosystems in eastern old-growth forests. In A. Barton & W. S. Keeton (Eds.), *Ecology and recovery of eastern old-growth forests* (pp. 159–178). Washington, DC: Island Press.

Watson, J. E. M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., ... Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, 2(4), 599–610. https://doi.org/10.1038/s41559-018-0490-x

Watson, J. E. M., Shanahan, D. F., Di Marco, M., Allan, J., Laurance, W. F., Sanderson, E. W., ... Venter, O. (2016). Catastrophic declines in wilderness areas undermine global environment targets. *Current Biology*, 26(21), 2929–2934. https://doi.org/10.1016/j.cub.2016.08.049

Zabel, F., Putzenlechner, B., & Mauser, W. (2014). Global agricultural land resources – A high resolution suitability evaluation and its perspectives until 2100 under climate change conditions. *PLoS ONE*, 9(9), e107522. https://doi.org/10.1371/journal.pone.0107522

BIOSKETCH

Francesco M. Sabatini is a forest ecologist. Within the framework of the Marie Skłodowska-Curie Project FORESTS & CO (Grant Agreement no. 658876), he established the Informal Network of Forest Scientists—F&CO-NET, as a means to bring together forest scientists and experts working on primary and old-growth forests. The main aim of this network is maintaining a harmonized geodatabase on the spatial distribution of primary forests in Europe and adjacent areas, and facilitating its use for non-commercial purposes, mainly academic and conservation-relevant research.

Author contributions: F.M.S. and T.K. designed the study. F.M.S. ran the statistical analyses. F.M.S., T.K. W.S.K., M.S., P-J.V., H.B., J.B., K.V., J.Sv. and M.S. drafted the first version of the manuscript. S.B., N.D., M.G., N.G., F.L., M.M., P.M., R.M., G.M., L.N., P.Ó., M.P., A.R., B.S., J.St., J.Sz., K.V., R.V., T.V. and T.Z. contributed data. All authors contributed to the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.