Available and missing data to model impact of climate change on European forests

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Abstract

Climate change is expected to cause major changes in forest ecosystems during the 21st century and beyond. To assess forest impacts from climate change, the existing empirical information must be structured, harmonised and assimilated into a form suitable to develop and test state-of-the-art forest and ecosystem models. The combination of empirical data collected at large spatial and long temporal scales with suitable modelling approaches is key to understand forest dynamics under climate change. To facilitate data and model integration, we identified major climate change impacts observed on European forest functioning and summarised the data available for monitoring and predicting such impacts. Our analysis of *c.* 120 forest-related databases (including information from remote sensing, vegetation inventories, dendroecology, palaeoecology, eddy-flux sites, common garden experiments and genetic techniques) and 50 databases of environmental drivers highlights a substantial degree of data availability and accessibility. However, some critical variables relevant to predicting European forest responses to climate change are only available at relatively short time frames (up to 10-20 years), including intra-specific trait variability, defoliation patterns, tree mortality and recruitment. Moreover, we identified data gaps or lack of data integration particularly in variables related to local adaptation and phenotypic plasticity, dispersal capabilities and physiological responses. Overall, we conclude that forest data availability across Europe is improving, but further efforts are needed to integrate, harmonise and interpret this data (i.e. making data useable for non-experts). Continuation of existing monitoring and networks schemes together with the

establishments of new networks to address data gaps is crucial to rigorously predict climate change impacts on European forests.

Highlights

- Harmonised freely-available data is crucial to model forest impacts on climate change.
- We summarise available datasets on forest functioning and underlying drivers.
- Data for key demographic mechanisms are available at the short-term at EU level.
- Lack of high-resolution harmonised EU data for genetic and physiological tree responses to climate change.
- Need for Pan-European data integration effort.

Keywords: climatic extremes; data accessibility; data integration; drivers; forest responses to climate change; harmonisation; open access.

1. Introduction

Changes in mean and extreme climatic conditions are affecting forest functioning worldwide (Frank *et al.*, 2015, EEA, 2017, Seidl *et al.*, 2017). Understanding and predicting these impacts is necessary for science-based decisions, but challenging because climate change interacts with other drivers of global change, such as rising atmospheric CO_2 (Cramer *et al.*, 2001), atmospheric deposition (de Vries *et al.*, 2014), land use change (Linares *et al.*, 2009, García-Valdés *et al.*, 2015), pests and invasive species (Krumm & Vitková, 2016, Liu *et al.*, 2017), and management and legacy effects (Baudena *et al.*, 2015, Motta *et al.*, 2015, Morales-Molino *et al.*, 2017a, Ruiz-Benito *et al.*, 2017b). Moreover, ecosystems react to climate change in complex ways, for example through stabilizing processes (Lloret *et al.*, 2012) such as positive biotic interactions (Ruiz-Benito *et al.*, 2017a) or local adaptation and phenotypic plasticity (Valladares *et al.*, 2014, Benito-Garzón *et al.*, 2019), but also with destabilizing non-linear responses and feedbacks that could trigger tipping points (Camarero *et al.*, 2015, Reyer *et al.*, 2015). To support the crucial role of forests in maintaining key ecosystem services decision-makers must adapt forests for the future (Messier *et al.*, 2013, IPCC, 2014). To aid this process, it is therefore critically important to rapidly increase our ability to predict forest responses and vulnerability to climate change (Urban *et al.*, 2016).

The use of empirical data at large spatial and/or long temporal extents in combination with suitable models is one of the most powerful tools for better understanding forest function, predicting vulnerability to climate change and assessing options for mitigation and adaptation (see e.g. Mouquet *et al.*, 2015). During the last few decades there has been a steady development in modelling techniques (Franklin *et al.*, 2016), aimed at better understanding and/or predicting species occurrence and abundance (e.g. Dormann *et al.*, 2012) or forests dynamics and functioning (e.g. gap models or Dynamic Global Vegetation Models –DGVMs–, see e.g. Bugmann *et al.*, 2001, Cramer *et al.*, 2001). Available models range from empirical to process-based approaches and from modelling local processes and dynamics up to global vegetation and general ecosystem models (Figure 1).

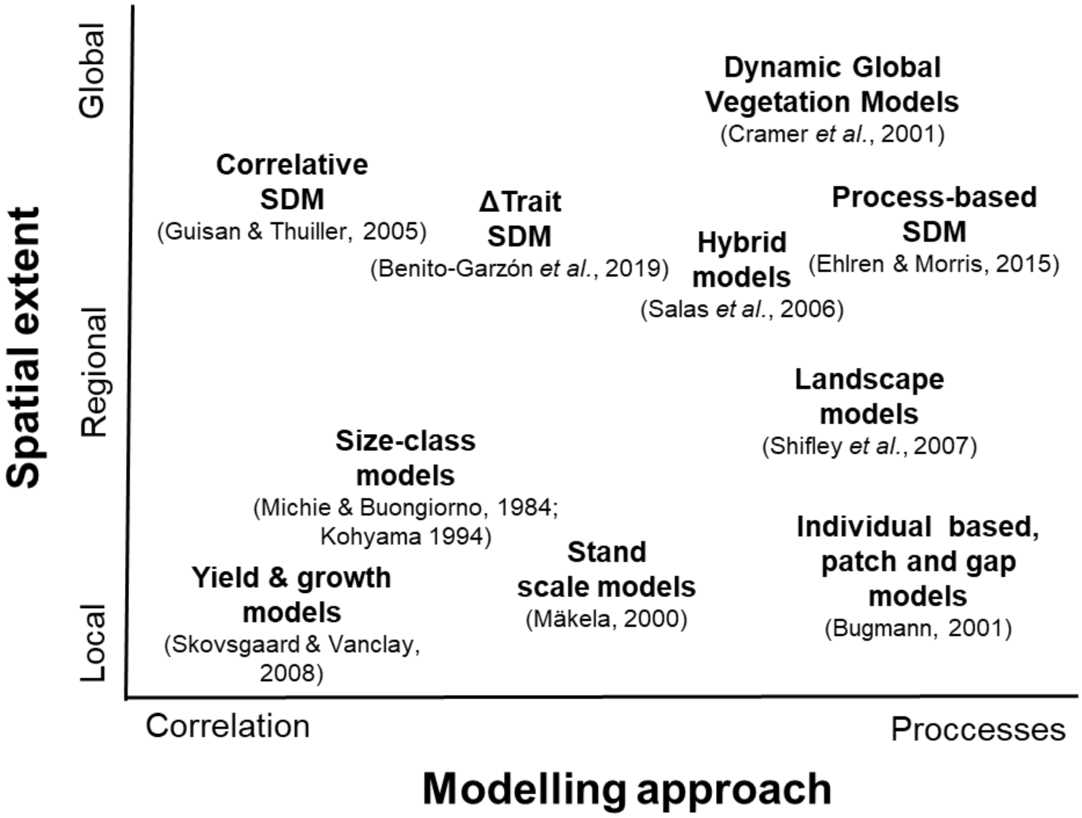

Figure 1. Existing model approaches to improve our understanding and prediction of climate change impacts. The models are classified according to spatial scale (local to global) and model type (correlative to process-based), with the position representing a relative ranking of the model types. SDM: Species Distribution Models. For each model type a review paper is associated if possible.

While there is a general agreement about the importance of assessing and predicting ecosystem responses to climate change (IPCC, 2014), there are multiple modelling approaches available to understand and predict climate change impacts quantitatively, designed to answer specific questions at different scales and using different data (Figure 1). The mechanisms and processes limiting model predictions at large geographical scales are under particularly intense debate (see e.g. Mouquet *et al.*, 2015, Franklin *et al.*, 2016, Seidl, 2017). Furthermore, forests are complex socio-ecological systems and predictions can be theory-limited because forest functioning depends on multiple spatial and temporal responses and scales that depend on species composition (García-Valdés *et al.*, 2018, Morin *et al.*, 2018) and may include thresholds or tipping points (Camarero *et al.*, 2015, Reyer *et al.*, 2015, Jump *et al.*, 2017), interactive effects (Scheffer *et al.*, 2001), phenological responses (Chuine & Régnière, 2017) and adaptation or time-dependent processes (Lloret *et al.*, 2012). A final challenge is the integration of models and data, and in particular the ability to adequately parameterise and test models at large spatial scales (Hartig *et al.*, 2012).

A key component to understand and predict forest responses to climate change is the extent, resolution and quality of associated environmental data such as climate, soils or nitrogen deposition. For example, environmental drivers are often themselves based on model outputs, not only of future predictions but also of past levels. Uncertainty about the future trajectory of the climate system, which largely depends on socio-economic development, can further impact prediction accuracy (Purves & Pacala, 2008, García-Valdés *et al.*, 2018). Moreover, much of the available data on observed impacts is not yet integrated and understood in the wider context of whole-ecosystem functioning. For example, climate change effects on shifting the time of flowering (but see Chuine *et al.*, 2016, Ascoli *et al.*, 2017b), tree mortality episodes (Greenwood *et al.*, 2017) or large wildfires (Pausas *et al.*, 2008) have been quantified but they are generally not included in many forest vulnerability assessments.

Impacts of climate change across European forests are occurring at all biological levels of organisation. At the tree level, decreased water availability or temperature stress might induce functional adjustments in respiration, water-use efficiency, hydraulic conductivity, resource allocation, reproductive efforts or phenology, and root-to-shoot allocation patterns (Penuelas *et al.*, 2011, Keenan *et al.*, 2013), which can ultimately influence reproduction, growth and mortality (Lambers *et al.*, 2008). At the population level, plant demography drives forest responses to climate change (Martínez-Vilalta & Lloret, 2016, Ruiz-Benito *et al.*, 2017b) depending on local adaptation to climate (Pedlar & McKenney, 2017; Fréjaville *et al.*, In review). Changes in tree growth and productivity are contingent on ecosystem-type and water availability (e.g. Vayreda *et al.*, 2012, Ruiz-Benito *et al.*, 2014) and individual responses to drought have been linked to long-term species composition changes (Galiano *et al.*, 2013, Martínez-Vilalta & Lloret, 2016). At the ecosystem level heat waves have been shown to have an overall depressing effect on net primary productivity (Ciais *et al.*, 2005, Reichstein *et al.*, 2013). The combination of increased atmospheric CO_2, nitrogen deposition, pollution and climate change is also considered a key factor in tree decline and ecosystem level responses (e.g. de Vries *et al.*, 2014). Furthermore, several studies indicate altitudinal and latitudinal shifts in species distribution and functional types across Europe (see Appendix A), attributable in many cases not to climate change alone, but with substantial interactions with herbivory release, secondary succession or forest management (Peñuelas & Boada, 2003, Ruiz-Benito *et al.*, 2017b).

To adequately identify potential risks and to establish future research and management priorities the scientific community, governments and other interested parties need well-structured, easily accessible and usable empirical data, often at large temporal and spatial scales. Multiple types, levels and sources of data are currently available, which can be harmonised to make compatible and comparable databases (GTOS, 1998), and prepare them to be suitable for model-based analyses. The aim of this paper is to support studies predicting forest responses and vulnerability to climate change by assessing the availability and accessibility of harmonised databases of forest functioning and underlying environmental drivers at the European scale. Firstly, based on a literature review, we identified the main types of forest response to climate change and the underlying interacting drivers. Then, based on expert knowledge, we researched the different data types available (genetic, eddy-flux measurement, experimental or observational field-techniques, tree-ring, palaeoecological and remote sensing techniques) to assess their ability to inform about climate change impacts (Figure 2). Additionally, we highlight the main data gaps and biases to predict climate change impacts on forests across Europe.

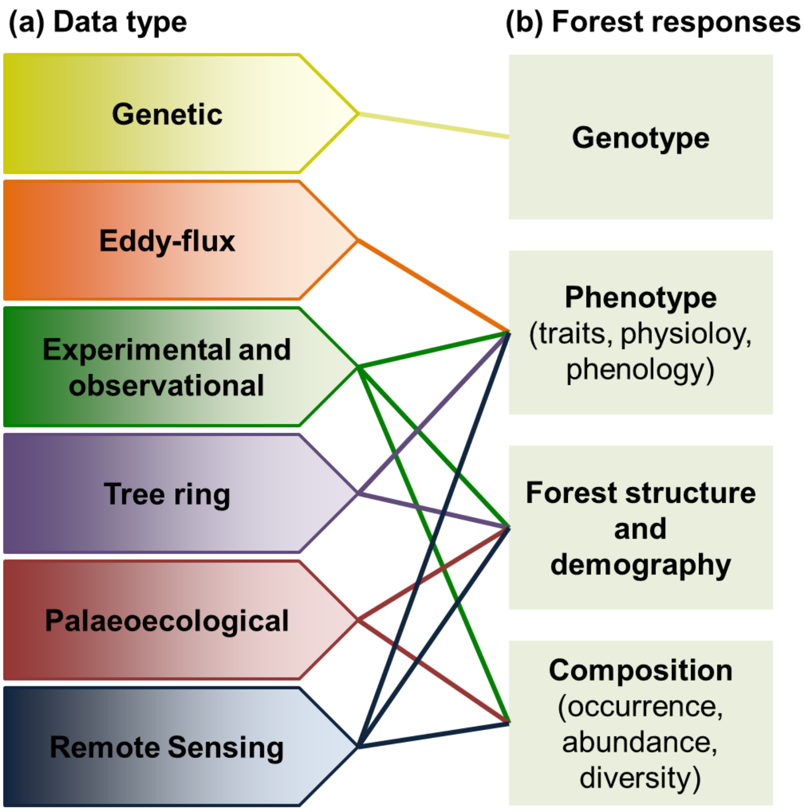

Figure 2. Relationships between (a) the data that can be used to detect and inform on (b) the biological levels at which forests may respond as a result of climate change.

2. Availability of data indicating forest responses to climate change

Forest responses to climate change are measured with different survey techniques that cover a range of spatial and temporal scales (see Figure 3 and Appendix B): genetic data show local adaptation to climate over generations; eddy flux measurements provide continuous data on local productivity at 0.5-1 hour resolution up to more than 20 years, vegetation inventories from local to regional scales cover show one -10 year changes across decadal to 100 year time-scale; dendrochronological data at local scales show yearly growth data over up to 5000 years; palaeoecological techniques at local scale cover long temporal scales (millennial data); and remote sensing data (RS) with high temporal and spatial resolution (continental for space-borne remote sensing, regional for airborne remote sensing and local for ground based remote sensing, Table 1), over a few years to multiple decades. The availability of these data varies from fully open-access to restricted-access (i.e. where the data is completely available for users or it is only available under request or a licence for a particular project, see Table 1).

Table 1. Data types available to inform about climate change impacts on forest functioning (see a complete list of each dataset including accessibility in Appendix B).

Data type *(specific measurement methods or examples)*	**Forest response type** *(indicator)*	**Spatial & temporal resolution** Extent (max. res) Span (step)	**Availability & accessibility** (strengths & challenges use)
Genetic data *(Genetic diversity and structure, common gardens and provenance trials, reciprocal transplant performance)*	Genotype, phenotype and composition *(genetic or phylogenetic diversity, local adaptation, plasticity)*	Regional to global (species ranges) -	From open- to restricted-access
Eddy flux data	Phenotype and drivers *(Carbon, water and energy fluxes; meteorological drivers and ecosystem state variables)*	Global (specific sites) Since 90s (hours)	Open-access (immediate forest responses to CC, inter-site comparison across vegetation types, sensitivity to climate factors, global synthesis studies)
Systematic vegetation inventories *(Regional, national or continental forest inventories, Long-term Research Networks)*	Demography, structure and composition *(Tree demography and wood/defoliation, forest structure, species occurrence or abundance; species or functional diversity)*	Regional-National-European (1 km or lower) Since 80s (up to decadal)	From open- to restricted-access (Data integration and management, no individual information of e.g. species-specific allometric equations or trait information)
Other vegetation inventories or experiments *(Field-based or experimental data)*	Phenotype, demography, structure and composition *(Traits, tree demography and wood/defoliation, forest structure, species occurrence or abundance; species or functional diversity)*	Regional-National-European (1 km or lower) Since 80s (up to decadal)	From open- to restricted-access (Data integration and management)
Tree ring data *(Tree growth or wood density)*	Demography and phenotype *(tree radial growth; wood density)*	Global (stand) 50-1000 yrs (year-season)	Open-access (No large-scale coverage, stand and/or tree characteristics often missing)

Data type *(specific measurement methods or examples)*	**Forest response type** *(indicator)*	**Spatial & temporal resolution** Extent (max. res) Span (step)	**Availability & accessibility** (strengths & challenges use)
Palaeoecological data *(Pollen or Macrofossil data)*	Structure and composition *(occurrence, species and functional group diversity, forest cover and change)*	Global (stand) 21,000 yrs. ago-present (Multi-decadal to millennial)	Open-access (Insights into past periods of abrupt climate change; multi-centennial timescale relevant for forest ecosystems; uneven spatial occurrence, sometimes quite localised; no large-scale spatial coverage at high resolution, relatively low time resolution)
Ground RS *(Terrestrial laser scanning, leaf spestoscopy)*	Structure *(height, dbh, biomass, fine-scale crown metrics and canopy gaps)*	Local (cm - ha) Since 00s (NA to decadal)	Restricted access, highly localised, no large-scale databases available (Easy sampling of fine spatial explicit measurements, require fieldwork and data processing)
Airborne RS *(Photogaphy, optical, LiDAR SAR)*	Structure *(canopy and sub-canopy including height, biomass, crown metrics)*	Local-Regional-National (cm) Since 00s (NA to decadal)	From open- to restricted access, highly localised (Detailed structural data, require data processing)
Space-borne RS* *(Landsat, AVHR; MODIS, SPOT, RADARSAT, ALOS PALSAR, SENTINEL)*	Demography, structure and composition *(forest cover/area, biomass, LAI, spectral diversity or phenology (NDVI, EVI), productivity)*	Global-continental (30 - 10 m) Since 80-90s (day-month)	Open-access (Computational challenges in interpreting the data and integrating them with existing ground data at different scales)

*RS: remote sensing data.

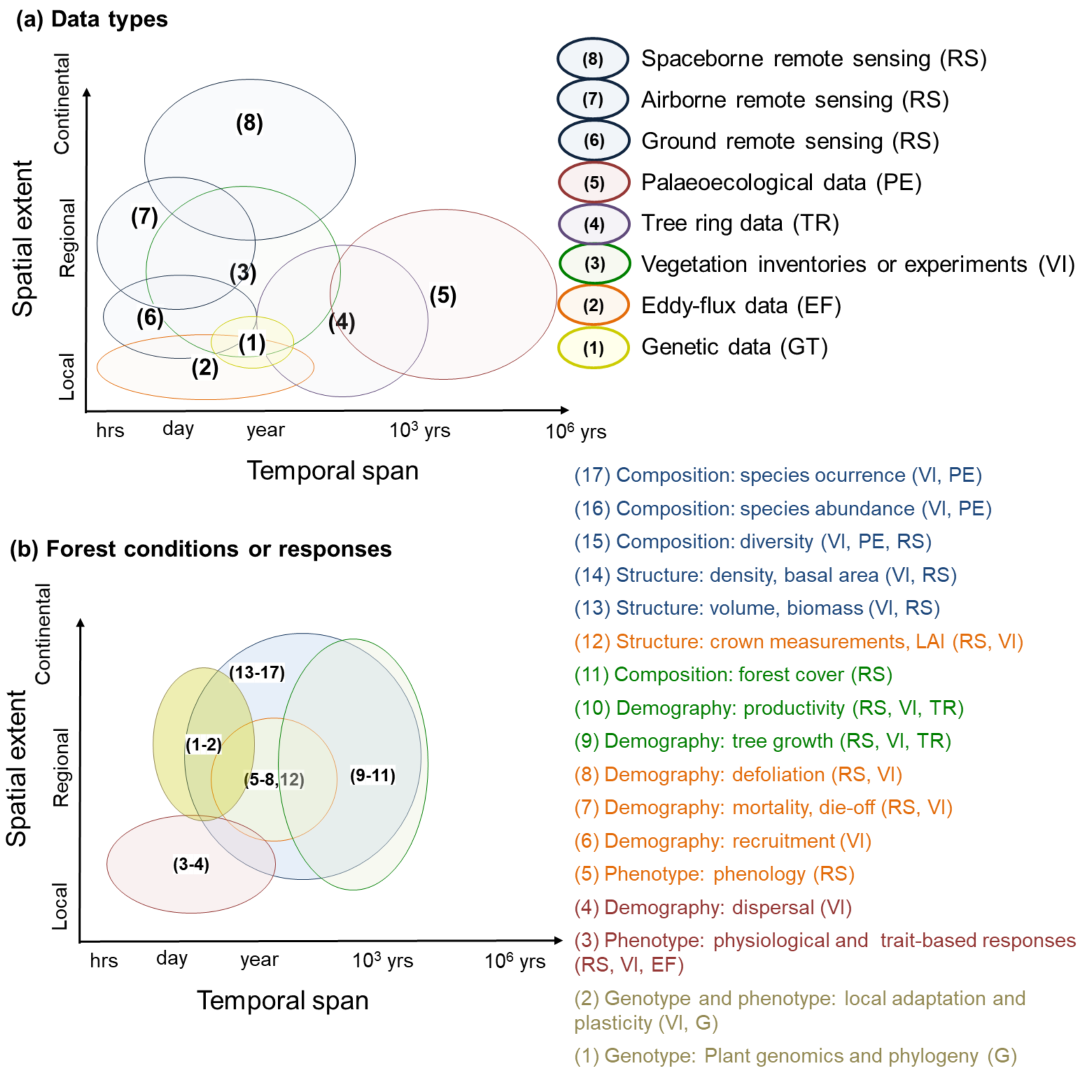

Figure 3. Harmonised picture of (a) data types and (b) forest conditions or responses to climate change depending on the spatial extent at which it is generally gathered (from local to regional and continental) and temporal span (i.e. from days up to 10^6 years), modified from Hartig *et al.* (2012). The position of the data type and forest condition o response is relative to provide a relative ranking within all data available. For each forest response the main data type is indicated as in Figure 2.

Genetic and phylogenetic diversity, local adaptation and plasticity

The capacity for **genetic and phylogenetic tree diversity** estimation is progressing rapidly thanks to ecological genomics (Holliday *et al.*, 2017). The increase in genomic data allow us to understand the association between allelic frequencies and environmental gradients (Fitzpatrick & Keller, 2015). Plant phylogenies are available for a large number of species (see e.g. (Zanne *et al.*, 2014), Appendix B) and it is being used to further estimate phylogenetic diversity at the European scale (van der Plas *et al.*, 2018). In Europe, adaptive genetic responses to climate using SNPs data are only available for a few species (Jaramillo-Correa *et al.*, 2015).

Local adaptation and plasticity are the main sources of intraspecific variation and should be considered when evaluating species responses to climate change because within-species ecological responses (abundance, biomass, community composition) are often greater than across species (Des Roches *et al.*, 2018) and predictions of species responses due to climate change can differ when intra-specific variability is taken into account (Moran *et al.*, 2016, Sánchez-Salguero *et al.*, 2018, Benito-Garzón *et al.*, 2019). Phenotypic measurements of fitness-related traits, such as tree diameter, height, phenology, growth and/or survival, from known genotypes at different locations can inform models about the amount of phenotypic trait variation attributable to local adaptation or phenotypic plasticity of populations (Moran *et al.*, 2016). Phenotypic variation has been traditionally measured in common gardens (i.e. genetic trials or provenance tests, see Appendix B) and has been established for most commercial tree species. It provides information about plasticity (i.e. one provenance planted in several common gardens with different environments) and local adaptation of populations (i.e. several provenances planted in one common garden, Savolainen *et al.*, 2013).

Plant phenotype: physiology, traits and phenology

Physiological parameters have traditionally been measured either in experimentally controlled conditions or in observational studies where the physiological outputs are highly dependent on environmental conditions, species interactions and adaptation mechanisms. Eddy flux measurements and new remote sensing products have the potential to further elucidate plant physiological responses. The Eddy covariance networks are particularly important for quantifying the spatial differences and temporal dynamics in CO_2 and water vapour exchange across large abiotic and biotic gradients. Estimates of water-use efficiency at large spatial extents and gross primary productivity (GPP) (e.g. Lasslop *et al.*, 2012, Wohlfahrt & Galvagno, 2017) can both be derived from eddy flux data. Meanwhile in many flux observation sites other important biometric measurements, such as soil respiration rates are reported as so-called ancillary data. These additional data allow for a more analytical view on the net fluxes and their partitioning into individual components of the forest carbon cycle, enabling the portioning of ecosystem respiration into heterotrophic and autotrophic components (see e.g. Rodeghiero & Cescatti, 2006, Brændholt *et al.*, 2018). The availability of new space-borne instruments enable measuring Sun Induced Chlorophyll Fluorescence (SIF), which offers a more direct link to plant physiology (Dobrowski *et al.*, 2005) and a promising way to quantify gross primary production from space (Grace *et al.*, 2007).

Global **phenology** and model parameterisation have long been estimated through Earth Observation methods (e.g. Justice *et al.*, 1985, Ahl *et al.*, 2006, Hmimina *et al.*, 2013, White *et al.*, 2014). Long-term passive optical data from programmes such as AVHRR, Landsat and MODIS (NASA) have been used to quantify decadal forest cover change on a near global scale (e.g. Hansen *et al.*, 2013). Such data have also been combined with ground measurements to detect climate-driven changes in temperate forest phenology over long time scales (Piao *et al.*, 2006, Keenan *et al.*, 2014) and phenological changes associated with the spread of invasive species (Ramsey *et al.*, 2005). However, data availability about phenological changes is scarce (see Appendix B), and a good understanding or predictive models of phenological responses are critical to further understand climate change consequences (Delpierre *et al.*, 2019).

Forest demography and structure

Forest demography can be assessed using vegetation inventories, tree ring data or remote sensing data. Regional, national and continental inventories (see Appendix B) are useful tools to estimate forest demographic processes such as tree growth, mortality and recruitment at the individual tree (Kunstler *et al.*, 2016, Neumann *et al.*, 2017) or plot level (Carnicer *et al.*, 2014, Ruiz-Benito *et al.*, 2017a) at regular intervals (often each c. 10 years). Recruitment data in systematic inventories have been successfully harmonised for saplings (height between 30 and 130 cm) across single censuses in Europe (Ruiz-Benito *et al.*, 2017a, van der Plas *et al.*, 2018), but recruitment data contain differential information about tree seedlings. In addition, recruitment data rarely contain time series records, dispersion information or individual tree information required to understand forest responses to climate change. Tree and site level radial growth at longer time spans and annual time steps can be obtained from tree ring and remote sensing data, which allow retrospective and prospective characterisations of forest responses, including forest resistance and resilience to short- and long-term climatic changes (Briffa *et al.*, 1998, Anderegg *et al.*, 2015, Gazol *et al.*, 2018). Re-surveyed plots from airborne remote sensing allow for monitoring of structural dynamics such as forest growth (Yu *et al.*, 2004) and large surveys can determine stand successional stage (Falkowski *et al.*, 2009). At stand level remote sensing allow also capturing long-term canopy defoliation and tree mortality (Senf *et al.*, 2018) (Table 1).

Forest structure can be characterised by **density, basal area, volume, biomass or crown metrics** at tree or plot level, obtained from vegetation inventories or remote sensing data (Figure 3, Table 1). Systematic vegetation inventories generally measure tree level diameter / height, allowing a direct calculation of plot level basal area or tree density and indirect volume or biomass estimates through the application of species-specific allometric equations (Montero *et al.*, 2005, Zianis *et al.*, 2005, Annighöfer *et al.*, 2016). Some National Forest Inventories measure the position of each tree within a plot enabling the calculation of distance-dependent competition indices and tree-to-tree interactions (Gómez-Aparicio *et al.*, 2011, Kunstler *et al.*, 2016), although small plots can lead to biased predictions (Hynynen & Ojansuu, 2003). Tree height and diameter are common inventory variables that can also be obtained from airborne LiDAR and ground-based remote sensing with higher accuracy than inventory based calculations (Zolkos *et al.*, 2013). LiDAR can provide sub-metre accuracy of surface heights (Lefsky *et al.*, 2002, Lee *et al.*, 2010), although accuracy can vary with canopy height and distribution (Hopkinson & Chasmer, 2009), ground slope (Breidenbach *et al.*, 2008) and sampling intensity (Hyyppä *et al.*, 2000). Low point density data can be used to calculate stem density, vertical foliage profile (Coops *et al.*, 2007) and basal area (Lee & Lucas, 2007), and is a promising method for above ground biomass measurement (Lefsky *et al.*, 2002, Mascaro *et al.*, 2011, Simonson *et al.*, 2016). There is enormous potential to develop large spatial and temporal scale datasets when combining these different data types, e.g. the spatially continuous height, age, biomass and carbon information derived from NFI and MODIS data (Mäkisara *et al.*, 2016, Moreno *et al.*, 2017).

Biomass or wood volume can be estimated at the global scale from space-borne remote sensing as passive microwave data (Liu *et al.*, 2015), passive optical data (e.g. from Landsat: Avitabile *et al.*, 2012), and SAR data from L-band (Mitchard *et al.*, 2011) and C-band instruments (Santoro *et al.*, 2010), but the latter methods typically require calibration using ground data (Rodríguez-Veiga *et al.*, 2017). SAR biomass estimates are calculated using backscatter coefficients related to wood volume scattering mechanisms and/or allometry using height estimates derived through polarimetric interferometry (PolInSAR; Mette *et al.*, 2004; (Le Toan *et al.*, 2011). Space borne LiDAR (ICESat GLAS) has been used to quantify biomass at the global scale (Simard *et al.*, 2011) and Popescu *et al.* (2011) suggest close correlations to airborne equivalents. The use of SAR for forest monitoring is likely to increase with the missions expected over the next decade (e.g. BIOMASS, NISAR and SAOCOM-1).

Space-borne remote sensing data provide long-term and large-scale information about **crown structure** as the **leaf area index (LAI)**. LAI is the projected leaf area relative to ground area (m^2 m^{-2}) and is a good proxy of plant response to water availability (Jump *et al.*, 2017). Satellite-derived LAI is generated with multispectral remote sensing reflectance data (Garrigues *et al.*, 2008). Long-term products are available at global scale with spatial resolution of 500 m or greater and temporal resolution from 8 days to 1 month (see Appendix B) as CYCLOPES (derived from SPOT, Baret *et al.*, 2007), GlobCarbon (derived from ERS, ENVISAT and SPOT, Deng *et al.*, 2006, Plummer *et al.*, 2007), and MODIS Leaf Area Index product (Knyazikhin *et al.*, 1998, Yang *et al.*, 2006).

Crown metrics can be estimated using airborne LiDAR with discrete return and high point density data (~ 8-20 points m^{-2} (Wu *et al.*, 2016), as crown volume (Korhonen *et al.*, 2013), vertical crown length (Lee *et al.*, 2010), crown diameter (Morsdorf *et al.*, 2004) and crown cover (Lee & Lucas, 2007). Full waveform LiDAR data can describe canopy vertical structural complexity (Nie *et al.*, 2017), including understory characterisation (Hancock *et al.*, 2017), crown morphology (Lindberg *et al.*, 2012) and height (Anderson-Teixeira *et al.*, 2015). A key parameter in many vegetation models, LiDAR derived LAI may be calculated using metrics of canopy structure, percentage canopy hits (Riaño *et al.*, 2004) and radiative transfer models (Tang *et al.*, 2012). This approach avoids the saturation issue inherent in passive optical estimates (Peduzzi *et al.*, 2012) and has been found to be more accurate than passive optical equivalents derived from MODIS data (Jensen *et al.*, 2011) and the GLOBCARBON product (Zhao & Popescu, 2009). Airborne SAR systems have the capacity to measure similar structural properties as LiDAR given their sensitivity to complex forest structure (Lausch *et al.*, 2017). Both correlative (Balzter *et al.*, 2007) and physically-based approaches (Ningthoujam *et al.*, 2016a) have been used to extract wood volume and vegetation height through interferometry (Neumann *et al.*, 2012). To date, SAR has quantified AGB, LAI (Peduzzi *et al.*, 2012), forest cover (Ningthoujam *et al.*, 2016b) and tree height (Ningthoujam *et al.*, 2016a). Unfortunately, currently there is little open-access airborne SAR data available (see Appendix B).

Fine scale spatially explicit **crown metrics** of stems and branches, as e.g. biomass or packing (Palace *et al.*, 2016), are not captured by traditional vegetation inventories. Terrestrial laser scanning (TLS) offers an efficient and accurate alternative to measure fine-scale forest attributes (Seidel *et al.*, 2015, Srinivasan *et al.*, 2015) such as height (Srinivasan *et al.*, 2015), diameter (Kankare *et al.*, 2013), biomass (Yu *et al.*, 2013, Calders *et al.*, 2015), canopy characteristics including crown width (Metz *et al.*, 2013, Srinivasan *et al.*, 2015) and canopy gaps (Seidel *et al.*, 2015). TLS is filling the gap between tree scale manual measurements and large-scale airborne LiDAR scanning (Srinivasan *et al.*, 2015), allowing upscaling airborne LiDAR measurements (Hancock *et al.*, 2017). However, TLS data is available locally because it requires specific fieldwork and the management of a high volume of data.

Species or functional occurrence, abundance and diversity

Species or functional type occurrence and abundance data can be calculated from data generally available in vegetation inventories, palaeoecological or remote sensing data. Data on actual species distribution in Europe tends to come from individual field-based observations (e.g. the worldwide database GBIF) and current knowledge (e.g. EUFORGEN or European maps from JRC, see a complete list in Appendix B). The systematic information from NFIs, gathered at regional or national level, and International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP forests gathered at European level) provides large-scale and long-term information about the state of forests (Appendix B). Systematic vegetation inventories provide detailed information on tree species occurrence and abundance (generally through basal area or density measurements) with a good spatial coverage within Europe across biomes but over a relatively short time span (see Appendix B and (Mauri *et al.*, 2017). Long-term changes in species occurrence and abundance in response to environmental variability can be assessed through fossil pollen and plant macrofossils data (Morales-Molino *et al.*, 2017b). Despite the uneven spatial distribution and the relatively low taxonomic and spatial/temporal resolution of palaeoecological data, the long time-span they usually cover allows to assess ecosystem dynamics during past periods of abrupt climate change (see Table 1), like the Younger Dryas-Holocene transition (rapid and marked warming dated *c.* 11700 years ago) or the 8.2 ka event (abrupt cooling centered at *c.* 8200 years ago). For instance, fossil pollen data have been successfully used to document changes in the distribution and abundance of the main plant genera of European vegetation over the last 15,000 years (Giesecke *et al.*, 2017). Similarly, plant macrofossils represent an interesting proxy to infer past distribution ranges as they often allow more precise plant identifications (even to species level) than pollen. Plant macrofossils are unequivocal indicators for past plant local presence due to their limited dispersal and are often directly dated therefore reducing uncertainty about their age (Birks & Birks, 2000). When reliable age estimates based on radiocarbon dates on terrestrial plant macrofossils and robust age-depth models are available, palaeoecological data allow accurate assessments on the responses of forest species to past climate changes, which can in turn be used to validate projected vegetation responses to future climate change.

Diversity metrics can be calculated from systematic vegetation inventories including tree and shrub richness, functional types or even functional or phylogenetic measurements when merged with trait/phylogenetic data (Ruiz-Benito *et al.*, 2017a) or specific field-based trait measurements (Vilà-Cabrera *et al.*, 2015). Plant trait information and plant phylogeny is available for a large number of plants (see e.g. the TRY database, try-db.org, Kattge *et al.*, 2011 or Zanne *et al.*, 2014, Appendix B) and it is being used to further estimate functional or phylogenetic diversity (Paquette & Messier, 2011).

Tree species diversity is not directly available from medium-resolution open-access Earth Observation data such as Landsat or MODIS. However, several studies have demonstrated the potential for predicting species richness and diversity from satellite-derived land cover and landscape complexity (e.g. Honnay *et al.*, 2003, Hernandez-Stefanoni & Ponce-Hernandez, 2004, Ma *et al.*, 2019), leaf traits (Moreno-Martínez *et al.*, 2018), or link species composition with forest dynamics (Huesca *et al.*, 2015). Other studies have used the Spectral Variation Hypothesis, which links spectral heterogeneity in the reflectance signal to environmental heterogeneity and therefore species diversity (Gould, 2000, Palmer *et al.*, 2002, Rocchini *et al.*, 2007, Rocchini *et al.*, 2016). Fine spatial resolution imagery has been used to identify tree species within forest ecosystems using classification approaches as e.g. combination of LiDAR with Pleiades data (e.g. Blázquez-Casado *et al.*, 2019), IKONOS (Carleer & Wolff, 2004, Dahdouh-Guebas *et al.*, 2004) or QuickBird (Neukermans *et al.*, 2008), but such data are usually complex to analyse or costly to obtain, limiting their use for mapping diversity at a regional or continental scale. Furthermore, structural and topographical information derived from airborne LiDAR can also provide information on tree species richness (Simonson *et al.*, 2012, Hernández-Stefanoni *et al.*, 2014, Lopatin *et al.*, 2016, Vaglio Laurin *et al.*, 2016).

3. Availability and accessibility of harmonised data at the European level

3.1. Forest responses

Harmonised data on forest conditions is available in multiple global and European scale databases (see Appendix B and a summary in Table 3) and range from open- to restricted-access (Table 2). For open-access databases citation and acknowledgment is usually mandatory. For more restricted datasets, the data managers or contributors can request authorship as a prerequisite for access (e.g. some harmonised NFI databases, common garden experiments, Table 2). Harmonised data at the European extent is generally of high quality, i.e. well-structured and documented. In some cases, data use does not require a high degree of expertise (e.g. processed or combined remote sensing products), but it requires managing large volumes of data. In others the use of data requires a medium-high degree of expertise as e.g. when managing unprocessed inventory data, tree ring or palaeoecological data (Table 2).

The data products of individual observational or experimental studies are increasingly being published online thanks to research networks, public repositories and more recently data-papers gaining increasing attraction. However, whether scientific data should be freely-accessible is under an intense debate (Gewin, 2016) and often there is a low replicability, even in journals with an established data policy (Stodden *et al.*, 2018). Data available and accessible at European level in data repositories or specific harmonisation initiatives cover many different data types such as trait information (e.g. TRY database, Kattge *et al.*, 2011), plant growth-related experimental responses to environment (i.e. Meta-phenomics, Poorter *et al.*, 2016), trait variation from common gardens or provenance tests (Robson *et al.*, 2018, Vizcaíno-Palomar *et al.*, 2019), provenance regions (12 tree species, SIG-Forest), seed masting (MASTREE, Ascoli *et al.*, 2017a), biomass and plant allometry (BADD, Falster *et al.*, 2015), forest conditions and demography (ICP forests, UNECE & ICP Forests Programme Co-ordinating Centre, 2016) and long-term experiments/observational data in regions of Europe including a large number of forest indicators (see ForestGEO, DEIMS or NOLTFOX, Appendix B).

Data harmonisation must include data standardisation protocols and specifically informing about data strengths and limitations (see Meyer *et al.*, 2016 for data of species occurrence, Franklin *et al.*, 2017). The main data strengths identified were taxonomic, spatial and temporal coverage, systematic data sampling and error identification and control (Table 2). The main data limitations were taxonomic, spatial or temporal uncertainty (i.e. ambiguous taxonomic data, spatial location or time since data collection, respectively); taxonomic, spatial or temporal coverage; multisource effects (i.e. different sampling techniques in input data such as plot size or sampling dates); or sampling effects (i.e. observation or measurement errors and over- or under-representation bias, see Table 2).

Table 2. Harmonised databases of forest responses at European extent. For each database we included the main data type ((a) genetic, (b) eddy flux, (c) vegetation inventories and experiments, (d) tree ring, (e) palaeoecological, and (f) remote sensing data), the accessibility (O: open-access, R: restricted-access) and attribution (A: if authorship can be requested/required). We show the main potential data limitations in the harmonised databases; and data availability, accessibility or attribution issues.

Database[*1]	Indicator (Data type)	Data strengths[*2]	Data limitations[*3]
TreeGenes, Hardwood genomic data, Genbank [(a), O-R, A]	Genetic diversity or sequences (Genetic data)	-	Multisource uncertainty
Benito-Garzón *et al.*, 2018, Robson *et al.*, 2018, Vizcaino-Palomar *et al.*, 2019, GnpIS, GENFORED, BeechCOSTe52 [(a), O-R]	Phenotypic plasticity and adaptation (Genetic conservation units, genetic entries, common gardens, provenance regions)	-	Taxonomic coverage (data not available for many species)
Meta-phenomics database [(c), R]	Phenotypic plasticity and adaptation (plant growth and performance)	-	Taxonomic and spatial coverage (data not available for all species and all climatic conditions)

Database[*1]	Indicator (Data type)	Data strengths[*2]	Data limitations[*3]
FLUXNET, CARBOEurope European Fluxes Database , and emerging ICOS carbon portal [(b), O]	Carbon, water and energy fluxes (Flux measurements)	Temporal and spatial coverage (standardised quality checked from more 600 towers since 80s comparable across time and sites)	Spatial coverage (localised sites)
GBIF, Euforgen, AFE, EFI Tree species map, TSDE, EVA, sPLOT, GFBI [(c),O-R]	Species occurrence or abundance (Vegetation inventories)	Spatial coverage (high resolution)	Temporal and spatial uncertainty (variable input data e.g. GBIF)
TRY database[(c)*4, O-R, A]	Functional traits (Field or experimental data)	Error identification and control	Temporal uncertainty and coverage, multi-source effects (multiple input data)
ICP forest[(c), R]	Forest demography and structure, some plant traits (Vegetation inventories)	Temporal coverage (available since 80s comparable across time and sites), systematic sampling at European level	Sampling effects (underrepresentation of extreme events)
National Forest Inventory harmonised (e.g. Occurrence data, GFBI, FUNDIV data) [(c), O-R, A]	Demography, forest structure, species occurrence and abundance, species diversity (Vegetation inventories)	Systematic sampling at national level	Temporal coverage (available since 80s but multiple inventories rarely harmonised), sampling effects (plot and time-intervals dependent on countries, under-representation of large trees and extreme responses)
International Tree-Ring Data Bank (ITRDB)[(d), FO]	Tree radial growth (tree ring data)	Temporal coverage (up to century)	Multisource effects (metadata improvements regarding tree size, age and site data) and sampling effects (mostly dominant and climate-sensitive trees sampled, individual and mean series of several trees),
European Pollen Database (EPD), Neotoma Paleoecology database[(e), O]	Long-term vegetation distribution and diversity (Palaeoecological data)	Temporal coverage (up to millennia)	Spatial coverage (limited sites), multisource (different time intervals) and sampling effects (under-representation of extreme responses)

Database[*1]	Indicator (Data type)	Data strengths[*2]	Data limitations[*3]
CORINE Land Cover, PALSAR and JRC forest maps, ESI Forest Map, JRC Forest Biomass increment, GLOBBIOMASS[(f), O]	Forest cover/area, biomass increment, habitat cover, forest change, carbon storage (Remote sensing)	Spatial coverage (high resolution)	Temporal coverage (short time span)

[*1]See details of the database regarding output; spatial and temporal scale; data availability and accessibility; websites and citations in Appendix S2.

[*2] All data is at least available at European extent. We classified data strengths as taxonomic, spatial and temporal coverage, systematic data sampling, error identification and control.

[*3] We classified data limitations as taxonomic, spatial and temporal uncertainty; taxonomic, spatial and temporal coverage; multisource or sampling effects.

[*4]Other trait databases area available and open-access generally for specific groups of traits or regions.

Genetic diversity (e.g. allelic frequency) data is not harmonised at the European level (but see Genbank database for specific queries of genes in plants, Table 2, Appendix B) and to our knowledge this type of data has not been used to study large-scale forest responses to climate (but see Jaramillo-Correa *et al.*, 2015). However, the improvements in the next-generation of sequencing technologies is increasing the availability of open-access databases ((Neale & Kremer, 2011), Table 3, Appendix B). Despite evidence that genotypes respond differently to climate change across the range of the species (e.g. Matías *et al.*, 2017) it can be difficult to measure genetic diversity and to incorporate it in predictive models of climate change effects (Kramer *et al.*, 2010). For example, neutral diversity does not show direct effects of genetic variation on fitness and, therefore, it is not informative about the adaptative or evolutionary potential of the species (Holderegger *et al.*, 2006). However, common gardens and provenance trials are an important source of knowledge on the effects of intra-specific genetic and phenotypic variation on species response to different climates (Savolainen *et al.*, 2013). Data harmonisation is not homogeneous for all data sources and the planting sites often do not include the entire distribution range of a given species (but see compilations for *Pinus pinea* L., *Pinus pinaster* Ait., *Pinus nigra* Arnold., *Abies* *alba* Mill. and *Fagus sylvatica* L., (Benito-Garzón *et al.*, 2018, Robson *et al.*, 2018, Vizcaíno-Palomar *et al.*, 2019)).

Eddy flux measurement networks are established on almost all continents (e.g. ASIAFLUX, AMERIFLUX, OZFLUX, EUROFLUX) with FLUXNET as a global network of networks with long-term research infrastructures (Papale *et al.*, 2012). Therefore, long-term harmonised high-quality data are available at both the global and European level (Table 2), providing detailed and standardised temporal information for specific towers across Europe (Aubinet *et al.*, 2012). Further methodological standardisation is emerging in new American (NEON) and European (ICOS) research infrastructures (Franz *et al.*, 2018).

The availability and accessibility of vegetation inventories depend on the database owner, varying from systematic vegetation inventories (e.g. NFI or ICP forests) to specific databases from research network or data-papers (see Appendix B). Several initiatives to harmonise NFIs are being undertaken, including COST Actions (Tomppo *et al.*, 2010), European projects such as e.g. BACCARA (http://www.baccara-project.eu/), FunDivEUROPE (http://www.fundiveurope.eu/, Baeten *et al.*, 2013) or DIABOLO (http://diabolo-project.eu/), and European Networks such as ENFIN (http://www.enfin.info/) or global Initiatives (GFBI, https://www.gfbinitiative.org). NFI data can be open- or restricted-access at country level but the data require error identification and harmonisation considerations (e.g. minimum tree size or basal area, management, (Ratcliffe *et al.*, 2016)) and harmonisation of heterogeneous databases as country-level NFIs should include standardisation steps to the final outputs. Harmonisation initiatives are resulting in the availability of NFI data at the European level, such as species occurrence (Mauri *et al.*,

2017) or forest structure (Moreno *et al.*, 2017). ICP plots include information about biodiversity and the health and vitality of forests, for example canopy affectation by defoliation or/and climate change interactions with other air pollutants (de Vries *et al.*, 2014, UNECE & ICP Forests Programme Co-ordinating Centre, 2016). The main data limitations are based on the temporal coverage of the data (available since the 1980s) and the importance of understanding the knowledge any sampling effects that might include the underrepresentation of large trees, differential plot sizes and time intervals.

Tree ring data are harmonised at global scale by NOAA's "International Tree Ring Data Bank" (ITRDB, Table 2 and Appendix B). The ITRDB provides long-term growth information (usually tree-ring widths but also tree-ring density data) at tree, stand and species levels that can be freely downloaded. However, most of the ITRDB data refer to classical dendrochronological data, i.e. cross-dated tree-ring series obtained from 10-20 dominant and climatically sensitive trees of the same species living in the same site, stand or tree population; often at climate-sensitive sites. Usually, authors analyse a chronology or mean series of the individual tree series from the same site. Certain considerations or data treatment is required to estimate climate impacts on the entire forest. First, the spatial and ecological extent of the chronologies is generally vague, because the size of the site is rarely defined (e.g. 0.5-1 ha). Second, sampling is often biased towards dominant big trees of similar age classes, from harsh sites where climate is the major constraint of radial growth, which can lead to biased estimates of forest productivity and carbon uptake. Third, there is an urgent requirement for better metadata for future tree-ring series to be uploaded to the ITRDB. For instance, tree size (d.b.h.) and age are rarely reported and stand information as basal area or tree density is usually lacking, but they are required to obtain useful estimates of radial growth (e.g.

basal area increment) and carbon fixation from the tree ring data. Tree-ring data from tropical forests are scarce at the ITRDB (partially due to the inherent difficulty of ring formation and cross-dating in these tropical sites), but ITRDB data have been successfully used in global analyses (e.g. Anderegg *et al.*, 2015).

Palaeoecological data at the European level are harmonised in the Neotoma Paleoecology Database (Neotoma) and the European Pollen Database (also accessible via Neotoma, see Appendix B). The main data-limitations relate to the spatial coverage (uneven distribution of sites across Europe), multisource and sampling effects (i.e. time interval can differ between sampling sites). Neotoma and the EPD are open-access standardized databases of published palaecological records to foster broad-scale (global or continental-scale) vegetation and land-use history studies (Williams *et al.*, 2018). Pollen-data can sometimes be difficult to use because: (1) Several plant species produce the same pollen type, which limits the estimation of plant diversity or specific species presence, but for woody taxa taxonomic resolution is usually high (except for most European deciduous oaks that cannot be distinguished by their pollen); (2) non-uniform representativeness of pollen distribution for vegetation distribution due to species-specific differences in pollen production, dispersal, deposition and preservation (e.g. anemophilous tree species with high pollen production and dispersal ability as e.g. *Pinus* sp. are often overrepresented, Broström et al., 2008). This bias can be corrected by using empirical species-specific pollen productivity estimates (PPEs, (Pearman *et al.*, 2008)); (3) pollen records mostly reflect vegetation structure and composition in an area whose size depends on the site and surface type (usually lakes and mires, (Sugita, 1994)). Macrofossil records are less abundant than pollen sequences in Europe, especially in the Mediterranean region. Similarly, macrofossil data availability is still limited compared with pollen data (see Neotoma, Appendix B) and most sequences are published as papers in specialised journals (e.g. Birks, 2003, Tinner & Kaltenrieder, 2005).

The availability of remote sensing information is vastly increasing thanks to recent technical advances (Kennedy *et al.*, 2014) but significant challenges remain to select, process and interpret data provided in order to make them easily usable for forest assessment and management (Table 2). Processed and combined products are now widely available and offer a great opportunity for use at European scale (Table 2), with the temporal coverage dependent on the specific platform and product (Appendix B). There is an increasing amount of open-access large-scale airborne LiDAR data across Europe (generally at regional scale) and the recently launched GEDI Mission will provide global coverage of spaceborne LiDAR (though over a relative short duration, Appendix B). TLS has the potential to move forward forest inventory datasets by providing new structural measurements at fine spatial scales (Liang *et al.*, 2016, White *et al.*, 2016) as well as new means to determine uncertainty of forest properties quantified by spaceborne and airborne methods.

3.2. Environmental data

Climate databases at European or global levels differ in spatio-temporal resolution and extent. Mean climatic conditions for the 20th century are often directly available at high spatial resolution and at global or European scales from databases such as Worldclim, E-OBS, Chelsa, Climatic Research Unit (CRU, see Table 3 and Appendix B) either for a certain period (e.g. WordClim data provide mean values for 1970-2000) or even monthly values for each year (e.g. E-OBS, CRU-TS, CRU-CL or CRU-SR, Appendix B). Temporal data on past temperature and precipitation (i.e. daily, monthly or yearly records) are available at the global and European level (e.g. CRU and E-OBS, respectively). There are new databases that combine the spatial resolution of WorldClim (1 km^2) with the temporal resolution of CRU (1901 - 2014) (Fréjaville & Benito Garzón, 2018), and European climate data has been downscaled at 1 km^2 for large temporal frameworks (i.e. 1951-2012, see Moreno & Hasenauer, 2016). There is also an R packags available to interpolate and downscale coarse climate data and obtain daily weather variables at landscape level (meteoland, De Cáceres *et al.*, 2018). Past climatic data can be used to calculate changes in climate (i.e. climatic anomalies based in annual data, e.g. Ruiz-Benito *et al.*, 2014). Drought effects are derived from climatic databases that are available at detailed spatial and/or temporal resolution (e.g. precipitation and drought indices; see Appendix B). Climatic data for future scenarios are available globally and bias-adjusted from the Intersectoral Impact Model Comparison Project (ISIMIP, Frieler *et al.*, 2017) and for Europe at different spatial resolutions from the EURO-CORDEX (https://www.hzg.de/ms/euro-cordex/) to CRU database or Wordclim (see Appendix B).

Other environmental drivers include topographic information (e.g. elevation, slope and aspect), soil classification and properties, disturbance and management information, atmospheric nitrogen or sulphur deposition and CO_2 concentrations, etc. Topographic information can be easily obtained from digital elevation models at different resolutions (e.g. from 2 m^2 to 1 km^2, Table 3). The Soil Grid dataset (https://soilgrids.org/) provides global information about site characteristics, physical and chemical properties (Appendix B). European Soils Data Centre (ESDC) and ISRIC

World Soil Information provide a wealth of soil science information, and the FAO a global soil organic carbon map, which is mostly open-access and directly downloadable at 1 km^2 (Appendix B). In addition to soil property and quality datasets, the ESDC hosts information on different soil functions and threats to soil functioning. Soil water content, temperature and snowpack has been estimated from 1979 to 2010 in the ERA-INTERIM/Land at a resolution of 0.125° (Balsamo *et al.*, 2015) and soil organic carbon is mapped at 1 km^2 resolution in the Global Soil Organic Carbon Map (Appendix B). However, potential drivers of forest responses to climate change as soil fertility or water retention (Wardle *et al.*, 2008) is not easily accessible at detailed resolution for the European extent.

Table 3. Data availability of environmental drivers across Europe. See a complete list of each dataset including accessibility in Appendix B. The accessibility is open-access upon citation and acknowledgement.

Data type	Example Databases	Information	Spatial resolution: Extent (max. res)	Temporal resolution	Challenges
Climate	Wordclim, CRU, NOAA, E-OBS, CHELSA, EuMedClim	Temperature and precipitation variables. Mean, annual & monthly data	EU (30’’)	Current and scenarios for past/future climate	Temporal data for the 20^{th} century and climate scenarios (e.g. monthly-yearly) at fine spatial resolution (e.g. 1 km or lower)
Atmospheric deposition	NOAA, IAC, WebDab	CO_2 and greenhouse gases concentration	EU level (0.1°)	50s-present	No spatial resolution in data
Digital Elevation Model	GTOP30	Altitude, slope, orientation, insolation	Global-Europe (2 m^2)	-	-
Soils	SoilGrid ESDA	Soil attributes and classification	Global-Europe (1 km^2)	-	Extract meaningful information for forest responses

Data type	Example Databases	Information	Spatial resolution: Extent (max. res)	Temporal resolution	Challenges
Disturbances	EFFIS, DFDE, EDP, EASIN	Area/perimeter burnt, pest, pathogens, exotic species	Europe-regional (0.25º)	Variable	No temporal information (only in remote sensing derived products)
Policy – management	CCDA, historical management and suitability for management	Protected sites, recent management	Europe (1 km^2)	NA	Missing data of forest management or legacy effects

Disturbances such as fires, pests or pathogens are major drivers of forest vulnerability that can strongly interact with climate change (e.g. Pausas & Keeley, 2009). Palaeoecological records often include charcoal data to reconstruct changes in fire activity through long timescales, which can be freely accessed and downloaded from the Global Charcoal Database (GCD; Power *et al.*, 2010) and Neotoma (Williams *et al.*, 2018). The Database of Forest Disturbances in Europe (DFDE; Appendix B) provides historical data on abiotic (i.e. wind and snow damage) and biotic (pathogens and insects) disturbance agents. DFDE has been used at the country-scale to empirically parameterise landscape models to predict future disturbance levels under different climate change scenarios (Seidl *et al.*, 2014). European initiatives to record and disseminate forest disturbance information include the EFI database, European Forest Fire Information System (EU-EFFIS) and the European Storms Catalogue (Appendix B). However, there is a considerable lack of geo-referenced data on pest and alien species in European forests and they are poorly linked to other databases on forest health such as ICP forests. Some initiatives involving citizen science are providing georeferenced data of forest pests at regional levels (e.g. http://www.alertaforestal.com/es/). The European Network of Alien Species (EASIN) provides access to records of alien species in Europe, via a mapping tool and a geo-referenced database of published scientific reports (EASIN-lit; Appendix B), although there are few records regarding forest ecosystems.

Data availability on forest management practices across Europe is limited because it is difficult to assign a management system to a forest stand based on signs of its recent management; long-term historical records are essential, but they are largely missing across most of Europe. NFIs are a valuable source of information on recent forest management but harmonising the descriptions across countries will remain challenging until a common classification system is used. The scarce information about management in vegetation inventories has generally led to harmonisation as a binary indicator field (managed or unmanaged), which provides only minimal information to aid in the understanding of forest responses to management (see e.g. Vayreda *et al.*, 2012). The Natura 2000 and Nationally Designated Areas (CDDA; see Appendix B) initiatives provide spatial information on the protected sites at the European level. These datasets cannot be used to infer the development of a particular management activity, but they could be used as an indication of different forest policy and management objectives. Given the limited availability of management information, historical reconstruction maps (e.g. McGrath *et al.*, 2015), forest management simulators (Härkönen *et al.*, 2019) and the Forest Management Map of European Forests (Hengeveld *et al.*, 2012) assesses the suitability of different forest management practices based on biotic, abiotic, and socioeconomic factors, which provide useful information for the development and assessment of management on forest resource models.

4. Considerations for harmonised data use in modelling forest responses to climate change

Harmonised and quality-controlled data at the European scale are needed for robust assessments of forest responses to climate change (Serra-Diaz *et al.*, 2018; Reyer *et al.*, 2019). We have demonstrated that data availability at the European extent has increased in the last few decades for a multitude of forest properties ranging from genetics to demography, forest structure and occurrence/abundance (Table 2) as well as for the potential interacting drivers of climate change (Table 3). We have also identified many open and semi-restricted databases across Europe, which will facilitate future integrative research on forest responses to climate change using multiple data sources.

We found several limitations that should be considered when developing models and frameworks based on the databases presented here, relating to spatial and temporal coverage and the effects of using multisource data and data with different sampling methodologies. Firstly, for specific forest properties data are not publicly available at high resolution or for many European species, particularly for intraspecific trait variability, adaptation and phenotypic variation, and physiological and dispersal responses. Secondly, the temporal coverage of key responses to climate change such as defoliation, mortality and recruitment is short (e.g. the main sources are vegetation inventories, which are only available since the 1980s). In addition, there are sampling issues such as the under-representation of big trees, no individual or harmonised data of tree recruitment and extreme responses might be under-represented when permanent plots of forest inventories are used. Thirdly, long-term data are available for forest cover and tree growth, but researchers should be aware of data limitations regarding spatial coverage (i.e. generally localised data) and sampling effects (e.g. selection of sensitive species/sites for study). The main limitations regarding underlying drivers of forest responses to climate change that we identified are the availability of meaningful and detailed soil information, long-term data about disturbances and forest management and legacy effects on forest functioning. Finally, most of the databases cannot deliver cause-effect mechanisms except emerging ecosystem experiments (see e.g. meta-phenomics database, Appendix B) and plant responses can differ in field-conditions (Poorter *et al.*, 2016).

Table 4. Main data limitations identified for each data type and how it can interact with modelling impacts to climate change.

Data limitations	Data type	Considerations for modelling	Example citations of databases or data use
Data not available at the entire EU extent at high resolution	Local adaptation, phenotypic plasticity or physiology	Biased prediction of climate change impacts due to prediction of more extreme responses or general species-specific physiological parameters	(Robson *et al.*, 2018, Benito-Garzón *et al.*, 2019)
No long-term or detailed data	Related to inventory data (tree mortality and recruitment) and management/legacy effects	Long-term forest dynamics biased due to lack of long-term or individual data for recruitment and mortality	(Baeten *et al.*, 2013, Evans & Moustakas, 2016)
Data available across Europe at specific sites	Long-term forest abundance or growth (palaeoecological data, tree ring and eddy flux responses) and disturbances	Not possible to predict climate change impacts for the entire European continent	(Anderegg *et al.*, 2015, Franz *et al.*, 2018, Williams *et al.*, 2018)
Extreme responses under- or over-represented	Forest inventory data or tree ring data	Unknown extreme forest responses or overestimation	(Anderegg *et al.*, 2015, Ruiz-Benito *et al.*, 2017b)

Extract meaningful and detailed information	Soil data and management	Missing interactions climate-soil and climate-legacy effects	(Härkönen *et al.*, 2019, Morán-Ordóñez *et al.*, 2019)
Cause-effect relationships are not available for a wide variety of conditions	Experimental data	Test forest responses for a variety of conditions	(Poorter *et al.*, 2016)

The lack of data on key mechanisms of forest responses to climate change either at high spatial resolution or long temporal span at the European scale can strongly hamper modelling of forest tree responses to climate change (Table 4). Local adaptation or physiological data at high spatial resolution is missing at large spatial scales and detailed resolution, but several efforts are being made to integrate available data such as ecological genomics to climate change predictions (Fitzpatrick & Keller, 2015) showing less alarming responses (Benito-Garzón *et al.*, 2019). Process-based models require a wide range of data to adequately parameterise and evaluate them, ideally consisting of a mix of stand or ecosystem conditions (e.g. stand structure, species abundance) and specific mechanisms or processes (e.g. photosynthesis data required in DGVM models, which ideally should come from controlled experiments, see Hartig *et al.*, 2012). In many cases, process-based models require large numbers of parameters of physiological responses to climate, but these values are often known only for special cases (Mäkelä *et al.*, 2000), or processes formulated for one region cannot be extrapolated to other climates or larger extents (Morales *et al.*, 2005). Detailed physiological, structural and ecosystem data are being gathered but rarely on the same plot or at European extent (Table 2). The lack of accurate data about traits and ecophysiological responses for individual species in e.g. hydraulic resistance, photosynthesis or respiration has led to the generalisation of the parameters for a given plant functional type, as e.g. depending on their shade-, flooding- or drought-tolerance and nitrogen requirements (Bugmann, 2001).

Detailed data on tree mortality or recruitment is available at large spatial scales, but it is generally missing at long temporal scales, which could bias long term predictions. In fact, there are diverging findings on tree mortality between observational data and model predictions (Allen *et al.*, 2015, Steinkamp & Hickler, 2015) and lack of tree recruitment data is likely to hamper model predictions (Evans & Moustakas, 2016). Furthermore, modelling forest responses to climate change might be affected by sampling bias due to the under representation of large trees (Vieilledent *et al.*, 2009) or extreme responses (Fisher *et al.*, 2008).

The short temporal span generally available in data is leading to predictions under constant conditions and the common use of space-for-time substitutions, where temporal patterns are inferred from a set of different aged sites (Pickett, 1989). Recent studies suggest that space-for-time predictions provide similar results to time-for-time predictions (Blois *et al.*, 2013, Rolo *et al.*, 2016). However, further research of forest responses and predictions using “space-for-time” substitution should be a priority because species are likely to show different responses to climate change due to adaptation (e.g. Benito-Garzón *et al.*, 2011) or legacy effects (Johnson & Miyanishi, 2008).

5. Conclusions: towards harmonised and freely available quality data to analyse and model forest responses to climate change

Despite the advances made, the main gap to better understanding and modelling of climate change impacts on European forests lies in the scarcity of high-quality, freely-available data with high spatial and temporal resolution that cover the main biological processes that are affected by climate change (e.g. dispersal, physiology, biotic interactions, demography, phenology and adaptation; Urban *et al.*, 2016, Cabral *et al.*, 2017). Open data exchange policies and research networks are leading to rapidly increasing accessibility of ecological and environmental data over large spatial extents. Data quality is often high, but observational data biases exist due to sampling effects, different time intervals and under-representation of extreme conditions. There are several examples of high-quality data at national, European or global extent that could serve as models for future data infrastructures. At the national and continental level forest inventories and the ICP databases are examples of systematically collected data that are widely used to asses forest vulnerability to climate (e.g. ICP database, UNECE & ICP Forests Programme Co-ordinating Centre, 2016). At global scales GFBI, ITRBD, FLUXNET data (Aubinet *et al.*, 2012) and the TRY database (Kattge *et al.*, 2011) combine high-quality data with established quality and assessment controls.

The increasing availability of data will further allow us to investigate complex mechanisms relevant for the assessment of forest impacts to climate change and to integrate them in a wide variety of forest models. The main data priorities to improve our understanding and model forest impacts to climate change are: (i) to maintain monitoring in existing data networks and start targeted new monitoring that addresses the identified gaps such as measuring climatic extremes and responses and to obtain long-term high-quality data on critical biological mechanisms driving forest responses to climate change, such as adaptation capacity, physiological responses, dispersal and regeneration, and mortality; (ii) to promote the availability and provision of harmonised freely-available databases and further develop the standardisation methods and quality assessment approaches; (iii) to increase discussion and networking between those scientists primarily involved in data collection and those in modelling and data integration; (iv) to encourage data integration methods from different sources, because they have the potential to use the existing information in the data more effectively and provide detailed information at large spatial and long temporal scales that can be used in different modelling frameworks.

6. Author contributions

F.H., A.L., A.M., C.P.O.R., P.R.-B., G.V., R.Y., M.A.Z Conceptualisation; J.C., P.R-B. Literature review; A.P-O., M.B.-G., H.J.F.O., J.J.C., A.S.J., A.I., E.L., C.M-M., P.R-B., S.R., G.V. Data review; all authors writing, review & editing.

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8. Supporting Material

Appendix A. Methods used for the literature review of climate change impacts on forests.

Appendix B. Databases available across Europe regarding forest responses and drivers of change including data description, spatial and temporal resolution, and accessibility information.

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