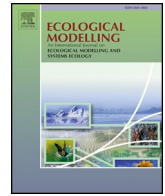




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## Available and missing data to model impact of climate change on European forests

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### ABSTRACT

Climate change is expected to cause major changes in forest ecosystems during the 21<sup>st</sup> 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,

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forest responses to climate change  
 harmonisation  
 open access

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.

## 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<sub>2</sub> (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 (Fig. 1).

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 (Fig. 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

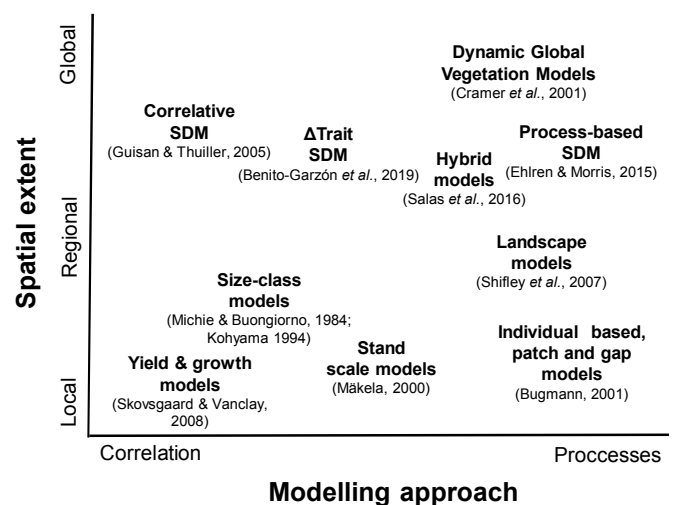


Fig. 1. Existing model approaches to improve our understanding and prediction of climate change impacts. The models are classified according to spatial scale (local to global) and model type (correlative to process-based), with the position representing a relative ranking of the model types. SDM: Species Distribution Models. For each model type a review paper is associated if possible (Ehrlén & Morris, 2015; Guisan and Thuiller, 2005; Kohyama, 1994; Michie and Buongiorno, 1984; Salas et al., 2016; Shifley et al., 2017; Skovsgaard and Vanclay, 2007).

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<sub>2</sub>, 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 (Fig. 2). Additionally, we highlight the main data gaps and biases to predict climate change impacts on forests across Europe.

## 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 Fig. 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).

### 2.1. 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).

### 2.2. 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.

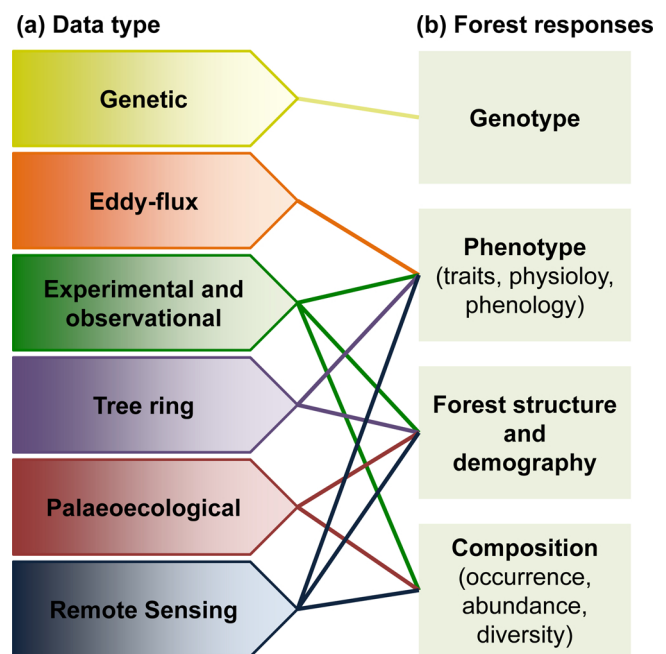
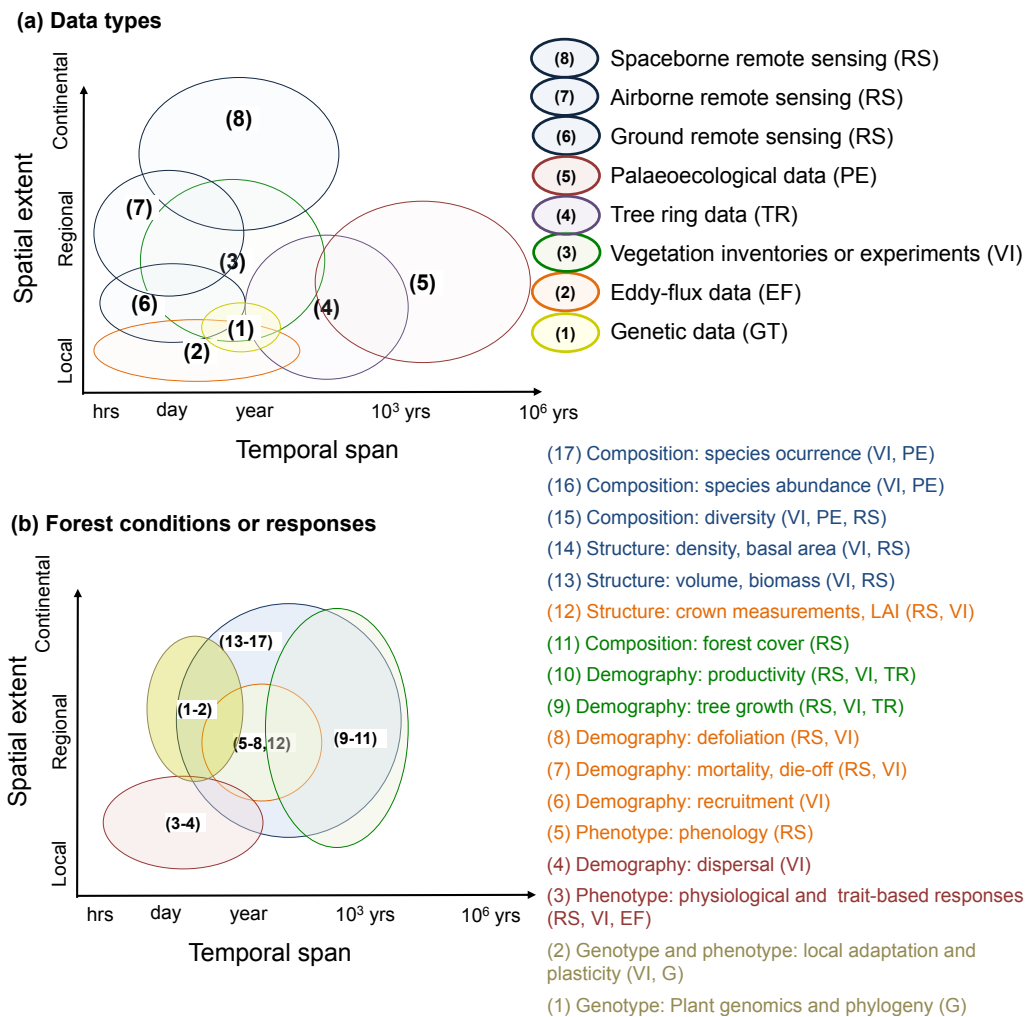


Fig. 2. Relationships between (a) the data that can be used to detect and inform on (b) the biological levels at which forests may respond as a result of climate change.



**Fig. 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<sup>6</sup> years), modified from [Hartig et al. \(2012\)](#). The position of the data type and forest condition or response is relative to provide a relative ranking within all data available. For each forest response the main data type is indicated as in [Fig. 2](#).

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<sub>2</sub> 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](#)).

### 2.3. 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

**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)
<b>Genetic data</b> (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
<b>Eddy flux data</b>	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)
<b>Systematic vegetation inventories</b> (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 80 s (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)
<b>Other vegetation inventories or experiments</b> (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 80 s (up to decadal)	From open- to restricted-access (Data integration and management)
<b>Tree ring data</b> (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)
<b>Palaeoecological data</b> (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)
<b>Ground RS</b> (Terrestrial laser scanning, leaf spetstoscopy)	Structure (height, dbh, biomass, fine-scale crown metrics and canopy gaps)	Local (cm - ha) Since 00 s (NA to decadal)	Restricted access, highly localised, no large-scale databases available (Easy sampling of fine spatial explicit measurements, require fieldwork and data processing)
<b>Airborne RS</b> (Photography, optical, LiDAR SAR)	Structure (canopy and sub-canopy including height, biomass, crown metrics)	Local-Regional-National (cm) Since 00 s (NA to decadal)	From open- to restricted access, highly localised (Detailed structural data, require data processing)
<b>Space-borne RS*</b> (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.

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 (Fig. 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 ( $\text{m}^2 \text{m}^{-2}$ ) 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 ( $\sim 8\text{--}20$  points  $\text{m}^{-2}$  (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 GLOBECARBON 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.

#### 2.4. 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

**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 <sup>1</sup>	Indicator (Data type)	Data strengths <sup>2</sup>	Data limitations <sup>3</sup>
TreeGenes, Hardwood genomic data, Genbank <sup>(a)</sup> , O-R, A	Genetic diversity or sequences (Genetic data)	-	Multisource uncertainty
Benito-Garzón et al., 2018, Robson et al., 2018, Vizcaíno-Palomar et al., 2019, GnpIS, GENFORED, BeechCOSTe52 <sup>(a)</sup> , 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 <sup>(c)</sup> , R	Phenotypic plasticity and adaptation (plant growth and performance)	-	Taxonomic and spatial coverage (data not available for all species and all climatic conditions)
FLUXNET, CARBOEurope European Fluxes Database, and emerging ICOS carbon portal <sup>(b)</sup> , O	Carbon, water and energy fluxes (flux measurements)	Temporal and spatial coverage (standardised quality checked from more 600 towers since 80 s comparable across time and sites)	Spatial coverage (localised sites)
GBIF, Euforgen, AFE, EFI Tree species map, TSDE, EVA, sPLOT, GFBI <sup>(c),O-R</sup>	Species occurrence or abundance (vegetation inventories)	Spatial coverage (high resolution)	Temporal and spatial uncertainty (variable input data e.g. GBIF)
TRY database <sup>(c),O-R, A</sup>	Functional traits (field or experimental data)	Error identification and control	Temporal uncertainty and coverage, multi-source effects (multiple input data)
ICP forest <sup>(c)</sup> , R	Forest demography and structure, some plant traits (vegetation inventories)	Temporal coverage (available since 80 s 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) <sup>(c)</sup> , O-R, A	Demography, forest structure, species occurrence and abundance, species diversity (vegetation inventories)	Systematic sampling at national level	Temporal coverage (available since 80 s 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) <sup>(d)</sup> , 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 Paleocology database <sup>(e)</sup> , 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)
CORINE Land Cover, PALSAR and JRC forest maps, ESI Forest Map, JRC Forest Biomass increment, GLOBBIOMASS <sup>(f)</sup> , O	Forest cover/area, biomass increment, habitat cover, forest change, carbon storage (remote sensing)	Spatial coverage (high resolution)	Temporal coverage (short time span)

<sup>1</sup> See details of the database regarding output; spatial and temporal scale; data availability and accessibility; websites and citations in Appendix S2.  
<sup>2</sup> 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.  
<sup>3</sup> We classified data limitations as taxonomic, spatial and temporal uncertainty; taxonomic, spatial and temporal coverage; multisource or sampling effects.  
<sup>4</sup> Other trait databases area available and open-access generally for specific groups of traits or regions.

**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 <sup>th</sup> century and climate scenarios (e.g. monthly-yearly) at fine spatial resolution (e.g. 1 km or lower)
Atmospheric deposition	NOAA, IAC, WebDab	CO <sub>2</sub> 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 <sup>2</sup> )	-	-
Soils	SoilGrid ESDA	Soil attributes and classification	Global-Europe (1 km <sup>2</sup> )	-	Extract meaningful information for forest responses
Disturbances	EFFIS, DFDE, EDP, EASIN	Area/perimeter burnt, pest, pathogens, exotic species	Europe-regional (0.25°)	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 <sup>2</sup> )	NA	Missing data of forest management or legacy effects

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).

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 adaptive 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 affection 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 palaeoecological 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 20<sup>th</sup> 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. WorldClim 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<sup>2</sup>) with the temporal resolution of CRU (1901 - 2014) ([Fréjaville & Benito Garzón, 2018](#)), and European climate data has been downscaled at 1 km<sup>2</sup> for large temporal frameworks (i.e. 1951-2012, see [Moreno & Hasenauer, 2016](#)). There is also an R package available to interpolate and downscale coarse climate data and obtain daily weather variables at landscape level (meteoland, [De Caceres 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<sub>2</sub> concentrations, etc. Topographic information can be easily obtained from digital elevation models at different resolutions (e.g. from 2 m<sup>2</sup> to 1 km<sup>2</sup>, [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<sup>2</sup> (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<sup>2</sup> 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.

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 geo-referenced 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.

### 3.2.1. 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).

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).

**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., 2017a,b)
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)

#### 4. 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 assess 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.

#### 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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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at [doi:https://doi.org/10.1016/j.ecolmodel.2019.108870](https://doi.org/10.1016/j.ecolmodel.2019.108870).

#### References

- Ahl, D.E., Gower, S.T., Burrows, S.N., Shabanov, N.V., Myneni, R.B., Knyazikhin, Y., 2006. Monitoring spring canopy phenology of a deciduous broadleaf forest using MODIS. *Remote Sensing of Environment* 104, 88–95.
- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6 art129.
- Annihöfer, P., Ameztegui, A., Ammer, C., et al., 2016. Species-specific and generic biomass equations for seedlings and saplings of European tree species. *European Journal of Forest Research* 135, 313–329.
- Anderegg, W.R.L., Schwalm, C., Biondi, F., et al., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349, 528–532.
- Anderson-Teixeira, K.J., Mcgarvey, J.C., Muller-Landau, H.C., et al., 2015. Size-related scaling of tree form and function in a mixed-age forest. *Functional Ecology* 29, 1587–1602.
- Ascoli, D., Maringer, J., Hacket-Pain, A., et al., 2017a. Two centuries of masting data for European beech and Norway spruce across the European continent. *Ecology*.
- Ascoli, D., Vacchiano, G., Turco, M., et al., 2017b. Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications* 8, 2205.
- Aubinet, M., Vesala, T., Papale, D., 2012. *Eddy covariance: a practical guide to measure data and analyses*. Springer.
- Avitabile, V., Baccini, A., Friedl, M.A., Schullius, C., 2012. Capabilities and limitations of Landsat and land cover data for aboveground woody biomass estimation of Uganda. *Remote Sensing of Environment* 117, 366–380.
- Baeten, L., Verheyen, K., Wirth, C., et al., 2013. A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics* 15, 281–291.
- Balsamo, G., Albergel, C., Beljaars, A., et al., 2015. ERA-Interim/Land: a global land surface reanalysis data set. *Hydrol. Earth Syst. Sci.* 19, 389–407.
- Balzer, H., Rowland, C.S., Saich, P., 2007. Forest canopy height and carbon estimation at Monks Wood National Nature Reserve, UK, using dual-wavelength SAR interferometry. *Remote Sensing of Environment* 108, 224–239.
- Baret, F., Hagolle, O., Geiger, B., et al., 2007. LAI, FAPAR and fCover CYCLOPES global products derived from VEGETATION: Part 1: Principles of the algorithm. *Remote Sensing of Environment* 110, 275–286.
- Baudena, M., Sánchez, A., Georg, C.-P., Ruiz-Benito, P., Rodríguez, M.A., Zavala, M.A., Rietkerk, M., 2015. Revealing patterns of local species richness along environmental gradients with a novel network tool. *Scientific Reports* 5, 11561.
- Benito-Garzón, M., Alfá, R., Robson, T.M., Zavala, M.A., 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography* 20, 766–778.
- Benito-Garzón, M., Fady, B., Davi, H., Vizcaíno-Palomar, N., Fernández-Manjarrés, J., 2018. Trees on the move: using decision theory to compensate for climate change at the regional scale in forest social-ecological systems. *Regional Environmental Change* 18, 1427–1437.
- Benito-Garzón, M., Robson, T.M., Hampe, A., 2019. ΔtraitSDMs: species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist* 222, 1757–1765.
- Birks, H.H., 2003. The importance of plant macrofossils in the reconstruction of Lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. *Quaternary Science Reviews* 22, 453–473.
- Birks, H.H., Birks, H.J.B., 2000. Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeography* 27, 31–35.
- Blázquez-Casado, A., Calama, R., Valbuena, M., Vergarechea, M., Rodríguez, F., 2019. Combining low-density LiDAR with satellite images to discriminate species in mixed Mediterranean forests. *Annals of Forest Sciences* 76, 57.
- Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences* 110, 9374–9379.
- Brändholt, A., Ibrom, A., Larsen, K.S., Pilegaard, K., 2018. Partitioning of ecosystem respiration in a beech forest. *Agricultural and Forest Meteorology* 252, 88–98.
- Breidenbach, J., Koch, B., Kändler, G., Kleusberg, A., 2008. Quantifying the influence of slope, aspect, crown shape and stem density on the estimation of tree height at plot level using lidar and InSAR data. *International Journal of Remote Sensing* 29, 1511–1536.
- Briffa, K.R., Schweingruber, F.H., Jones, P.D., et al., 1998. Trees tell of past climates: but are they speaking less clearly today? *Philosophical Transactions: Biological Sciences*

- 353, 65–73.
- Bugmann, H., 2001. A review of forest gap models. *Climatic Change* 51, 259–305.
- Cabral, J.S., Valente, L., Hartig, F., 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. *Ecography* 40, 267–280.
- Calders, K., Newnham, G., Burt, A., et al., 2015. Nondestructive estimates of above-ground biomass using terrestrial laser scanning. *Methods in Ecology and Evolution* 6, 198–208.
- Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., Vicente-Serrano, S.M., 2015. To die or not to die: early warnings of tree dieback in response to a severe drought. *Journal of Ecology* 103, 44–57.
- Carleer, A., Wolff, E., 2004. Exploitation of very high resolution satellite data for tree species identification. *Photogrammetric Engineering & Remote Sensing* 70, 135–140.
- Carnicer, J., Coll, M., Pons, X., Ninyerola, M., Vayreda, J., Peñuelas, J., 2014. Large-scale recruitment limitation in Mediterranean pines: the role of *Quercus ilex* and forest successional advance as key regional drivers. *Global Ecology and Biogeography* 23, 371–384.
- Chuine, I., Bonhomme, M., Legave, J.-M., García De Cortázar-Atauri, L., Charrier, G., Lacoine, A., Améglio, T., 2016. Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology* 22, 3444–3460.
- Chuine, I., Régnière, J., 2017. Process-based models of phenology for plants and animals. *Annual Review of Ecology, Evolution, and Systematics* 48, 159–182.
- Ciais, P., Reichstein, M., Viovy, N., et al., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437, 529–533.
- Coops, N.C., Hilker, T., Wulder, M.A., St-Onge, B., Newnham, G., Siggins, A., Trofymow, J.A., 2007. Estimating canopy structure of Douglas-fir forest stands from discrete-return LiDAR. *Trees* 21, 295.
- Cramer, W., Bondeau, A., Woodward, F.I., et al., 2001. Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology* 7, 357–373.
- Dahdouh-Guebas, F., Van Hiel, E., Chan, J.C.W., Jayatissa, L.P., Koedam, N., 2004. Qualitative distinction of congeneric and introgressive mangrove species in mixed patchy forest assemblages using high spatial resolution remotely sensed imagery (IKONOS). *Systematics and Biodiversity* 2, 113–119.
- De Caceres, M., Martin-StPaul, N., Turco, M., Cabon, A., Granda, V., 2018. Estimating daily meteorological data and downscaling climate models over landscapes. *Environmental Modelling and Software* 108, 186–196.
- De Vries, W., Dobbertin, M.H., Solberg, S., Van Dobben, H.F., Schaub, M., 2014. Impacts of acid deposition, ozone exposure and weather conditions on forest ecosystems in Europe: an overview. *Plant and Soil* 380, 1–45.
- Delpierre, N., Lireux, S., Hartig, F., et al., 2019. Chilling and forcing temperatures interact to predict the onset of wood formation in Northern Hemisphere conifers. *Global Change Biology* 25, 1089–1105.
- Deng, F., Chen, J.M., Plummer, S., Chen, M., Pisek, J., 2006. Algorithm for global leaf area index retrieval using satellite imagery. *IEEE Transactions on Geoscience and Remote Sensing* 44, 2219–2229.
- Des Roches, S., Post, D.M., Turley, N.E., et al., 2018. The ecological importance of intraspecific variation. *Nature Ecology & Evolution* 2, 57–64.
- Dobrowski, S.Z., Pushnik, J.C., Zarco-Tejada, P.J., Ustin, S.L., 2005. Simple reflectance indices track heat and water stress-induced changes in steady-state chlorophyll fluorescence at the canopy scale. *Remote Sensing of Environment* 97, 403–414.
- Dormann, C.F., Schymanski, S.J., Cabral, J., et al., 2012. Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography* 39, 2119–2131.
- Eea, 2017. In: Agency, E.E. (Ed.), *Climate change, impacts and vulnerability in Europe 2016: an indicator-based report*, Luxembourg.
- Ehrlén, J., Morris, W.F., 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters* 18, 303–314.
- Evans, M.R., Moustakas, A., 2016. A comparison between data requirements and availability for calibrating predictive ecological models for lowland UK woodlands: learning new tricks from old trees. *Ecology and Evolution* 6, 4812–4822.
- Falkowski, M.J., Evans, J.S., Martinuzzi, S., Gessler, P.E., Hudak, A.T., 2009. Characterizing forest succession with lidar data: An evaluation for the Inland Northwest, USA. *Remote Sensing of Environment* 113, 946–956.
- Falster, D.S., Duursma, R.A., Ishihara, M.I., et al., 2015. BAAD: a Biomass And Allometry Database for woody plants. *Ecology* 96, 1445.
- Fisher, J.L., Hurr, G.C., Thomas, R.Q., Chambers, J.Q., 2008. Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecology Letters* 11, 554–563.
- Fitzpatrick, M.C., Keller, S.R., 2015. Ecological genomics meets community-level modelling of biodiversity: mapping the genomic landscape of current and future environmental adaptation. *Ecology Letters* 18, 1–16.
- Frank, D.A., Reichstein, M., Bahn, M., et al., 2015. Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Global Change Biology* 21, 2861–2880.
- Franklin, J., Serra-Diaz, J.M., Syphard, A.D., Regan, H.M., 2016. Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences* 113, 3725–3734.
- Franklin, J., Serra-Diaz, J.M., Syphard, A.D., Regan, H.M., 2017. Big data for forecasting the impacts of global change on plant communities. *Global Ecology and Biogeography* 26, 6–17.
- Franz, D., Acosta, M., Altimir, N., et al., 2018. Towards long-term standardised carbon and greenhouse gas observations for monitoring Europe's terrestrial ecosystems: a review. *International Agrophysics* 32, 439–455.
- Fréjaville, T., Benito Garzón, M., 2018. The EuMedClim Database: Yearly Climate Data (1901–2014) of 1 km Resolution Grids for Europe and the Mediterranean Basin. *Frontiers in Ecology and Evolution* 6.
- Fréjaville, T., Vizaño-Palomar, N., Fady, B., Kremer, A., Benito Garzón, M., 2019. Range margin populations show high climate adaptation lags in European trees. *Global Change Biology*.
- Frieler, K., Lange, S., Piontek, F., et al., 2017. Assessing the impacts of 1.5 °C global warming – simulation protocol of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP2b). *Geosci. Model Dev.* 10, 4321–4345.
- Galiano, L., Martínez-Vilalta, J., Eugenio, M., Granzow-De La Cerda, Í., Lloret, F., 2013. Seedling emergence and growth of *Quercus* spp. following severe drought effects on a *Pinus sylvestris* canopy. *Journal of Vegetation Science* 24, 580–588.
- García-Valdés, R., Bugmann, H., Morin, X., 2018. Climate change-driven extinctions of tree species affect forest functioning more than random extinctions. *Diversity and Distributions* 24, 906–918.
- García-Valdés, R., Svenning, J.-C., Zavala, M.A., Purves, D.W., Araújo, M.B., 2015. Evaluating the combined effects of climate and land-use change on tree species distributions. *Journal of Applied Ecology* 52, 902–912.
- Garrigues, S., Lacaze, R., Baret, F., et al., 2008. Validation and intercomparison of global Leaf Area Index products derived from remote sensing data. *Journal of Geophysical Research: Biogeosciences* 113.
- Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., et al., 2018. Forest resilience to drought varies across biomes. *Global Change Biology* 24, 2143–2158.
- Gewin, V., 2016. Data sharing: an open mind on open data. *Nature* 529, 117–119.
- Giesecke, T., Brewer, S., Finsinger, W., Leydet, M., Bradshaw, R.H.W., 2017. Patterns and dynamics of European vegetation change over the last 15,000 years. *Journal of Biogeography* n/a/n/a.
- Gómez-Aparicio, L., García-Valdés, R., Ruiz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for management under global change. *Global Change Biology* 17, 2400–2414.
- Gould, W., 2000. Remote sensing of vegetation, plant species richness and regional biodiversity hotspots. *Ecological Applications* 10, 1861–1870.
- Grace, J., Nichol, C., Disney, M., Lewis, P., Quaife, T., Bowyer, P., 2007. Can we measure terrestrial photosynthesis from space directly, using spectral reflectance and fluorescence? *Global Change Biology* 13, 1484–1497.
- Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., et al., 2017. Tree mortality across forest biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters* 20, 539–553.
- Gtos, 1998. *GTOS Data and Information Management Plan*. Global Terrestrial Observation System. FAO.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8, 993–1009.
- Hancock, S., Anderson, K., Disney, M., Gaston, K.J., 2017. Measurement of fine-spatial-resolution 3D vegetation structure with airborne waveform lidar: Calibration and validation with voxelised terrestrial lidar. *Remote Sensing of Environment* 188, 37–50.
- Hansen, M.C., Potapov, P.V., Moore, R., et al., 2013. High-resolution global maps of 21<sup>st</sup>-Century forest cover change. *Science* 342, 850–853.
- Härkönen, S., Neumann, M., Mues, V., et al., 2019. A climate-sensitive forest model for assessing impacts of forest management in Europe. *Environmental Modelling & Software* 115, 128–143.
- Hartig, F., Dyke, J., Hickler, T., Higgins, S.I., O'hara, R.B., Scheiter, S., Huth, A., 2012. Connecting dynamic vegetation models to data – an inverse perspective. *Journal of Biogeography* 39, 2240–2252.
- Hengeveld, G.M., Nabuurs, G.-J., Didion, M., Van Den Wyngaert, I., Clerckx, A.P.P.M., Schelhaas, M.-J., 2012. A forest management map of European forests. *Ecology and Society* 17.
- Hernández-Stefanoni, J., Dupuy, J., Johnson, K., et al., 2014. Improving Species Diversity and Biomass Estimates of Tropical Dry Forests Using Airborne LiDAR. *Remote Sensing* 6, 4741.
- Hernandez-Stefanoni, J.L., Ponce-Hernandez, R., 2004. Mapping the spatial distribution of plant diversity indices in a tropical forest using multi-spectral satellite image classification and field measurements. *Biodiversity & Conservation* 13, 2599–2621.
- Hmimina, G., Dufrene, E., Pontailier, J.Y., et al., 2013. Evaluation of the potential of MODIS satellite data to predict vegetation phenology in different biomes: An investigation using ground-based NDVI measurements. *Remote Sensing of Environment* 132, 145–158.
- Holderegger, R., Kamm, U., Gugerli, F., 2006. Adaptive vs. neutral genetic diversity: implications for landscape genetics. *Landscape Ecology* 21, 797–807.
- Holliday, J.A., Aitken, S.N., Cooke, J.E.K., et al., 2017. Advances in ecological genomics in forest trees and applications to genetic resources conservation and breeding. *Molecular Ecology* 26, 706–717.
- Honnay, O., Piessens, K., Van Landuyt, W., Hermly, M., Gulinck, H., 2003. Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. *Landscape and Urban Planning* 63, 241–250.
- Hopkinson, C., Chasmer, L., 2009. Testing LiDAR models of fractional cover across multiple forest ecotones. *Remote Sensing of Environment* 113, 275–288.
- Huesca, M., Merino-De-Miguel, S., Eklundh, L., et al., 2015. Ecosystem functional assessment based on the “optical type” concept and self-similarity patterns: An application using MODIS-NDVI time series autocorrelation. *International Journal of Applied Earth Observation and Geoinformation* 43, 132–148.
- Hynynen, J., Ojansuu, R., 2003. Impact of plot size on individual-tree competition measures for growth and yield simulators. *Canadian Journal of Forest Research* 33, 455–465.
- Hyypää, J., Hyypää, H., Inkinen, M., Engdahl, M., Linko, S., Zhu, Y.-H., 2000. Accuracy comparison of various remote sensing data sources in the retrieval of forest stand attributes. *Forest Ecology and Management* 128, 109–120.

- IPCC, 2014. Climate change 2014: impacts, adaptation, and vulnerability. Cambridge, United Kingdom and New York, USA.
- Jaramillo-Correa, J.-P., Rodríguez-Quilón, I., Grivet, D., et al., 2015. Molecular Proxies for Climate Maladaptation in a Long-Lived Tree *Pinus pinaste* Aiton, Pinaceae). *Genetics* 199, 793–807.
- Jensen, J.L.R., Humes, K.S., Hudak, A.T., Vierling, L.A., Delmelle, E., 2011. Evaluation of the MODIS LAI product using independent lidar-derived LAI: A case study in mixed conifer forest. *Remote Sensing of Environment* 115, 3625–3639.
- Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. *Ecology Letters* 11, 419–431.
- Jump, A.S., Ruiz-Benito, P., Greenwood, S., et al., 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Global Change Biology* 23, 3742–3757.
- Justice, C.O., Townshend, J.R.G., Holben, B.N., Tucker, C.J., 1985. Analysis of the phenology of global vegetation using meteorological satellite data. *International Journal of Remote Sensing* 6, 1271–1318.
- Kankare, V., Holopainen, M., Vastaranta, M., et al., 2013. Individual tree biomass estimation using terrestrial laser scanning. *ISPRS Journal of Photogrammetry and Remote Sensing* 75, 64–75.
- Kattge, J., Diaz, S., Lavorel, S., et al., 2011. TRY - a global database of plant traits. *Global Change Biology* 17, 2905–2935.
- Keenan, T.F., Gray, J., Friedl, M.A., et al., 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Clim. Change* 4, 598–604.
- Keenan, T.F., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P., Richardson, A.D., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499, 324–327.
- Kennedy, R.E., Andréfouët, S., Cohen, W.B., et al., 2014. Bringing an ecological view of change to Landsat-based remote sensing. *Frontiers in Ecology and the Environment* 12, 339–346.
- Knyazikhin, Y., Kranigk, J., Myneni, R.B., Panforyor, O., Gravenhorst, G., 1998. Influence of small-scale structure on radiative transfer and photosynthesis in vegetation canopies. *Journal of Geophysical Research: Atmospheres* 103, 6133–6144.
- Kohyama, T., 1994. Size-structure-based models of forest dynamics to interpret population- and community-level mechanisms. *Journal of Plant Research* 107, 107–116.
- Korhonen, L., Vauhkonen, J., Virolainen, A., Hovi, A., Korpela, I., 2013. Estimation of tree crown volume from airborne lidar data using computational geometry. *International Journal of Remote Sensing* 34, 7236–7248.
- Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M.T., De Winter, W., 2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change—Range, abundance, genetic diversity and adaptive response. *Forest Ecology and Management* 259, 2213–2222.
- Krumm, F., Vitková, L., 2016. Introduced tree species in European forests: opportunities and challenges. *European Forest Institute*.
- Kunstler, G., Falster, D., Coomes, D.A., et al., 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529, 204–207.
- Lambers, H., Chapin Iii, F.S., Pons, T.L., 2008. *Plant physiological responses*. Springer, New York.
- Lasslop, G., Migliavacca, M., Bohrer, G., et al., 2012. On the choice of the driving temperature for eddy-covariance carbon dioxide flux partitioning. *Biogeosciences* 9, 5243–5259.
- Lausch, A., Erasmi, S., King, D., Magdon, P., Heurich, M., 2017. Understanding Forest Health with Remote Sensing-Part II—A Review of Approaches and Data Models. *Remote Sensing* 9, 129.
- Le Toan, T., Quegan, S., Davidson, M.W.J., et al., 2011. The BIOMASS mission: Mapping global forest biomass to better understand the terrestrial carbon cycle. *Remote Sensing of Environment* 115, 2850–2860.
- Lee, A.C., Lucas, R.M., 2007. A LiDAR-derived canopy density model for tree stem and crown mapping in Australian forests. *Remote Sensing of Environment* 111, 493–518.
- Lee, H., Slatton, K.C., Roth, B.E., Cropper, W.P., 2010. Adaptive clustering of airborne LiDAR data to segment individual tree crowns in managed pine forests. *International Journal of Remote Sensing* 31, 117–139.
- Lefsky, M.A., Cohen, W.B., Parker, G.G., Harding, D.J., 2002. Lidar Remote Sensing for Ecosystem Studies. *BioScience* 52, 19–30.
- Liang, X., Kankare, V., Hyyppä, J., et al., 2016. Terrestrial laser scanning in forest inventories. *ISPRS Journal of Photogrammetry and Remote Sensing* 115, 63–77.
- Linares, J.C., Camarero, J.J., Carreira, J.A., 2009. Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. *Global Ecology and Biogeography* 18, 485–497.
- Lindberg, E., Olofsson, K., Holmgren, J., Olsson, H., 2012. Estimation of 3D vegetation structure from waveform and discrete return airborne laser scanning data. *Remote Sensing of Environment* 118, 151–161.
- Liu, Y., Oduor, A.M.O., Zhang, Z., et al., 2017. Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology* 23, 3363–3370.
- Liu, Y.Y., Van Dijk, A.I.J.M., De Jeu RaM, Canadell, J.G., McCabe, M.F., Evans, J.P., Wang, G., 2015. Recent reversal in loss of global terrestrial biomass. *Nature Clim. Change* 5, 470–474.
- Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J., Valladares, F., 2012. Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology* 18, 797–805.
- Lopatín, J., Dolos, K., Hernández, H.J., Galleguillos, M., Fassnacht, F.E., 2016. Comparing Generalized Linear Models and random forest to model vascular plant species richness using LiDAR data in a natural forest in central Chile. *Remote Sensing of Environment* 173, 200–210.
- Ma, X., Mahecha, M.D., Migliavacca, M., et al., 2019. Inferring plant functional diversity from space: the potential of Sentinel-2. *Remote Sensing of Environment* 233, 111368.
- Mäkelä, A., Landsberg, J., Ek, A.R., et al., 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiology* 20, 289–298.
- Mäkisara, K., Katila, M., Peräsaari, J., Tomppo, E., 2016. The Multisource National Forest Inventory of Finland - methods and results from 2013. Helsinki.
- Martínez-Vilalta, J., Lloret, F., 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. *Global and Planetary Change* 144, 94–108.
- Mascaro, J., Detto, M., Asner, G.P., Muller-Landau, H.C., 2011. Evaluating uncertainty in mapping forest carbon with airborne LiDAR. *Remote Sensing of Environment* 115, 3770–3774.
- Matías, L., Linares, J.C., Sánchez-Miranda, Á., Jump, A.S., 2017. Contrasting growth forecasts across the geographical range of Scots pine due to altitudinal and latitudinal differences in climatic sensitivity. *Global Change Biology* n/a-n/a.
- Mauri, A., Strona, G., San-Miguel-Ayanz, J., 2017. EU-Forest, a high-resolution tree occurrence dataset for Europe. *Scientific Data* 4, 160123.
- Mcgrath, M.J., Luysaert, S., Meyfroidt, P., et al., 2015. Reconstructing European forest management from 1600 to 2010. *Biogeosciences* 12, 4291–4316.
- Messier, C., Puettmann, K.J., Coates, D.K., 2013. *Managing forests as complex adaptive systems. Building resilience to the challenges of global change*. London & New York.
- Metz, J., Seidel, D., Schall, P., Scheffer, D., Schulze, E.-D., Ammer, C., 2013. Crown modeling by terrestrial laser scanning as an approach to assess the effect of above-ground intra- and interspecific competition on tree growth. *Forest Ecology and Management* 310, 275–288.
- Meyer, C., Weigelt, P., Kreft, H., 2016. Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecology Letters* 19, 992–1006.
- Michie, B.R., Buongiorno, J., 1984. Estimation of a matrix model of forest growth from re-measured permanent plots. *Forest Ecology and Management* 8, 127–135.
- Mitchard, E.T.A., Saatchi, S.S., Lewis, S.L., et al., 2011. Measuring biomass changes due to woody encroachment and deforestation/degradation in a forest-savanna boundary region of central Africa using multi-temporal L-band radar backscatter. *Remote Sensing of Environment* 115, 2861–2873.
- Montero, G., Ruiz-Peinado, R., Muñoz, M., 2005. *Producción de biomasa y fijación de CO<sub>2</sub> por los bosques españoles*, Madrid.
- Morales-Molino, C., Colombaroli, D., Valbuena-Carabaña, M., Tinner, W., Salomón, R.L., Carrion, J.S., Gil, L., 2017a. Land-use history as a major driver for long-term forest dynamics in the Sierra de Guadarrama National Park (central Spain) during the last millennia: implications for forest conservation and management. *Global and Planetary Change* 152, 64–75.
- Morales-Molino, C., Tinner, W., García-Antón, M., Colombaroli, D., 2017b. The historical demise of *Pinus nigra* forests in the Northern Iberian Plateau (south-western Europe). *Journal of Ecology* 105, 634–646.
- Morales, P., Sykes, M.T., Prentice, I.C., et al., 2005. Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. *Global Change Biology* 11, 2211–2233.
- Morán-Ordóñez, A., Rocas-Díaz, J.V., Otsu, K., et al., 2019. The use of scenarios and models to evaluate the future of nature values and ecosystem services in Mediterranean forests. *Regional Environmental Change* 19, 415–428.
- Moran, E.V., Hartig, F., Bell, D.M., 2016. Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology* 22, 137–150.
- Moreno, A., Hasenauer, H., 2016. Spatial downscaling of European climate data. *International Journal of Climatology* 36, 1444–1458.
- Moreno, A., Neumann, M., Hasenauer, H., 2017. Forest structures across Europe. *Geoscientia Data Journal* 4, 17–28.
- Moreno-Martínez, Á., Camps-Valls, G., Kattge, J., et al., 2018. A methodology to derive global maps of leaf traits using remote sensing and climate data. *Remote Sensing of Environment* 218, 69–88.
- Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., Bugmann, H., 2018. Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports* 8, 5627.
- Morsdorf, F., Meier, E., Kötz, B., Itten, K.I., Dobbertin, M., Allgöwer, B., 2004. LiDAR-based geometric reconstruction of boreal type forest stands at single tree level for forest and wildland fire management. *Remote Sensing of Environment* 92, 353–362.
- Motta, R., Garbarino, M., Berretti, R., Meloni, F., Nosenzo, A., Vacchiano, G., 2015. Development of old-growth characteristics in uneven-aged forests of the Italian Alps. *European Journal of Forest Research* 134, 19–31.
- Mouquet, N., Lagadeuc, Y., Devictor, V., et al., 2015. Predictive ecology in a changing world. *Journal of Applied Ecology* 52, 1293–1310.
- Neale, D.B., Kremer, A., 2011. Forest tree genomics: growing resources and applications. *Nature Reviews Genetics* 12, 111.
- Neukermans, G., Dahdouh-Guebas, F., Kairo, J.G., Koedam, N., 2008. Mangrove species and stand mapping in Gazi bay (Kenya) using quickbird satellite imagery. *Journal of Spatial Ecology* 53, 75–86.
- Neumann, M., Mues, V., Moreno, A., Hasenauer, H., Seidl, R., 2017. Climate variability drives recent tree mortality in Europe. *Global Change Biology* 23, 4788–4797.
- Neumann, M., Saatchi, S.S., Ulander, L.M.H., Franssen, J.E.S., 2012. Assessing Performance of L- and P-Band Polarimetric Interferometric SAR Data in Estimating Boreal Forest Above-Ground Biomass. *IEEE Transactions on Geoscience and Remote Sensing* 50, 714–726.
- Nie, S., Wang, C., Zeng, H., Xi, X., Li, G., 2017. Above-ground biomass estimation using airborne discrete-return and full-waveform LiDAR data in a coniferous forest. *Ecological Indicators* 78, 221–228.
- Ningthoujam, R., Balzter, H., Tansey, K., et al., 2016a. Airborne S-Band SAR for Forest

- Biophysical Retrieval in Temperate Mixed Forests of the UK. *Remote Sensing* 8, 609.
- Ningthoujam, R., Tansey, K., Balzter, H., et al., 2016b. Mapping Forest Cover and Forest Cover Change with Airborne S-Band Radar. *Remote Sensing* 8, 577.
- Palace, M., Sullivan, F.B., Ducey, M., Herrick, C., 2016. Estimating tropical forest structure using a terrestrial Lidar. *PLOS ONE* 11, e0154115.
- Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P.S., Wohlgenuth, T., 2002. Quantitative tools for perfecting species lists. *Environmetrics* 13, 121–137.
- Papale, D., Agarwal, D.A., Baldochi, D., Cook, R.B., Fisher, J.B., Ingen, C.V., 2012. Database maintenance, data sharing policy, collaboration. In: Aubinet, M., Vesala, T., Papale, D. (Eds.), *Eddy Covariance: A practical guide to measurement and data analyses*. Springer, London, New York.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20, 170–180.
- Pausas, J.C., Llovet, J., Rodrigo, A., Vallejo, R., 2008. Are wildfires a disaster in the Mediterranean basin? - A review. *International Journal of Wildland Fire* 17, 713–723.
- Pausas, J.G., Keeley, J.E., 2009. A burning story: the role of fire in the history of life. *BioScience* 59, 593–601.
- Pearman, P.B., Randin, C.F., Broennimann, O., et al., 2008. Prediction of plant species distributions across six millennia. *Ecology Letters* 11, 357–369.
- Pedlar, J.H., McKenney, D.W., 2017. Assessing the anticipated growth response of northern conifer populations to a warming climate. *Scientific Reports* 7, 43881.
- Peduzzi, A., Wynne, R.H., Thomas, V.A., Nelson, R.F., Reis, J.J., Sanford, M., 2012. Combined Use of Airborne Lidar and DBInSAR Data to Estimate LAI in Temperate Mixed Forests. *Remote Sensing* 4, 1758.
- Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny Mountains (NE Spain). *Global Change Biology* 9, 131–140.
- Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Global Ecology and Biogeography* 20, 597–608.
- Piao, S., Fang, J., Zhou, L., Ciais, P., Zhu, B., 2006. Variations in satellite-derived phenology in China's temperate vegetation. *Global Change Biology* 12, 672–685.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), *Long-term studies in ecology: approaches and alternatives*. Springer, New York.
- Plummer, S., Arino, O., Ranera, F., et al., 2007. The GLOBCARBON initiative global biophysical products for terrestrial carbon studies. 2007 IEEE International Geoscience and Remote Sensing Symposium.
- Poorter, H., Fiorani, F., Pieruschka, R., et al., 2016. Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytologist* 212, 838–855.
- Popescu, S.C., Zhao, K., Neunenschwander, A., Lin, C., 2011. Satellite lidar vs. small footprint airborne lidar: Comparing the accuracy of aboveground biomass estimates and forest structure metrics at footprint level. *Remote Sensing of Environment* 115, 2786–2797.
- Power, M.J., Marlon, J.R., Bartlein, P.J., Harrison, S.P., 2010. Fire history and the Global Charcoal Database: A new tool for hypothesis testing and data exploration. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291, 52–59.
- Purves, D., Pacala, S., 2008. Predictive models of forest dynamics. *Science* 320, 1452.
- Ramsey, E., Rangoonwala, A., Nelson, G., Ehrlich, R., 2005. Mapping the invasive species, Chinese tallow, with EO1 satellite Hyperion hyperspectral image data and relating tallow occurrences to a classified Landsat Thematic Mapper land cover map. *International Journal of Remote Sensing* 26, 1637–1657.
- Ratcliffe, S., Liebergesell, M., Ruiz-Benito, P., et al., 2016. Modes of functional biodiversity control on tree productivity across the European continent. *Global Ecology and Biogeography* 25, 251–262.
- Reichstein, M., Bahn, M., Ciais, P., et al., 2013. Climate extremes and the carbon cycle. *Nature* 500, 287–295.
- Reyer, C.P.O., Brouwers, N., Rammig, A., et al., 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *Journal of Ecology* 103, 5–15.
- Reyer, C.P.O., Silveyra Gonzalez, R., Dolos, K., et al., 2019. The PROFOUND database for evaluating vegetation models and simulating climate impacts on forests. V.0.1.12. GFZ Data Services. .
- Riaño, D., Valladares, F., Condés, S., Chuvieco, E., 2004. Estimation of leaf area index and covered ground from airborne laser scanner (Lidar) in two contrasting forests. *Agricultural and Forest Meteorology* 124, 269–275.
- Robson, T., Benito Garzón, M., BeechCOSTe52 Database Consortium, 2018. Phenotypic trait variation measured on European genetic trials of *Fagus sylvatica* L. *Scientific Data* 5, 269–275.
- Rocchini, D., Boyd, D.S., Féret, J.-B., et al., 2016. Satellite remote sensing to monitor species diversity: potential and pitfalls. *Remote Sensing in Ecology and Conservation* 2, 25–36.
- Rocchini, D., Ricotta, C., Chiarucci, A., 2007. Using satellite imagery to assess plant species richness: the role of multispectral systems. *Applied Vegetation Science* 10, 325–331.
- Rodeghiero, M., Cescatti, A., 2006. Indirect partitioning of soil respiration in a series of evergreen forest ecosystems. *Plant and Soil* 284, 7–22.
- Rodríguez-Veiga, P., Wheeler, J., Louis, V., Tansey, K., Balzter, H., 2017. Quantifying forest biomass carbon stocks from space. *Current Forestry Reports* 3, 1–18.
- Rolo, V., Olivier, P.I., Guldemond, RaR, Van Aarde, R.J., 2016. Validating space-for-time substitution in a new-growth coastal dune forest. *Applied Vegetation Science* 19, 235–243.
- Ruiz-Benito, P., Madrigal-González, J., Ratcliffe, S., et al., 2014. Stand structure and recent climate change constrain stand basal area change in European forests: a comparison across boreal, temperate and Mediterranean biomes. *Ecosystems* 17, 1439–1454.
- Ruiz-Benito, P., Ratcliffe, S., Jump, A., et al., 2017a. Functional diversity underlies demographic responses to environmental variation in European forests. *Global Ecology and Biogeography* 26, 128–141.
- Ruiz-Benito, P., Ratcliffe, S., Zavala, M.A., et al., 2017b. Climate- and successional-related changes in functional composition of European forests are strongly driven by tree mortality. *Global Change Biology* 23, 4162–4176.
- Salas, C., Gregoire, T.G., Craven, D.J., Gilibert, H., 2016. Forest growth modelling: the state of the art. *Bosque* 37, 3–12.
- Sánchez-Salguero, R., Camarero, J.J., Rozas, V., et al., 2018. Resist, recover or both? Growth plasticity in response to drought is geographically structured and linked to intraspecific variability in *Pinus pinaster*. *Journal of Biogeography* 45, 1126–1139.
- Santoro, M., Beer, C., Cartus, O., et al., 2010. The BIOMASAR algorithm: An approach for retrieval of forest growing stock volume using stacks of multi-temporal SAR data. *Proceedings of ESA Living Planet Symposium*.
- Savolainen, O., Lascoux, M., Merilä, J., 2013. Ecological genomics of local adaptation. *Nature Reviews Genetics* 14, 807.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Seidel, D., Ammer, C., Puettmann, K., 2015. Describing forest canopy gaps efficiently, accurately, and objectively: New prospects through the use of terrestrial laser scanning. *Agricultural and Forest Meteorology* 213, 23–32.
- Seidl, R., 2017. To model or not to model, that is no longer the question for ecologists. *Ecosystems* 20, 222–228.
- Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerke, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Clim. Change* 4, 806–810.
- Seidl, R., Thom, D., Kautz, M., et al., 2017. Forest disturbances under climate change. *Nature Clim. Change* 7, 395–402.
- Senf, C., Pflugmacher, D., Zhiqiang, Y., et al., 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications* 9, 4978.
- Serra-Diaz, J.M., Enquist, B.J., Maitner, B., Merow, C., Svenning, J.-C., 2018. Big data of tree species distributions: how big and how good? *Forest Ecosystems* 4, 30.
- Shifley, S.R., He, H.S., Lischke, H., et al., 2017. The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. *Landscape Ecology* 32, 1307–1325.
- Simard, M., Pinto, N., Fisher, J.B., Baccini, A., 2011. Mapping forest canopy height globally with spaceborne lidar. *Journal of Geophysical Research: Biogeosciences* 116.
- Simonson, W., Ruiz-Benito, P., Valladares, F., Coomes, D., 2016. Modelling above-ground carbon dynamics using multi-temporal airborne lidar: insights from a Mediterranean woodland. *Biogeosciences* 13, 961–973.
- Simonson, W.D., Allen, H.D., Coomes, D.A., 2012. Use of an Airborne Lidar System to Model Plant Species Composition and Diversity of Mediterranean Oak Forests Utilización de un Sistema Lidar Aerotransportado para Modelar la Composición y Diversidad de Especies de Plantas en Bosques Mediterráneos de Roble. *Conservation Biology* 26, 840–850.
- Skovsgaard, J.P., Vanclay, J.K., 2007. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. *Forestry: An International Journal of Forest Research* 81, 13–31.
- Srinivasan, S., Popescu, S., Eriksson, M., Sheridan, R., Ku, N.-W., 2015. Terrestrial Laser Scanning as an Effective Tool to Retrieve Tree Level Height, Crown Width, and Stem Diameter. *Remote Sensing* 7, 1877.
- Steinkamp, J., Hickler, T., 2015. Is drought-induced forest dieback globally increasing? *Journal of Ecology* 103, 31–43.
- Stodden, V., Seiler, J., Ma, Z., 2018. An empirical analysis of journal policy effectiveness for computational reproducibility. *Proceedings of the National Academy of Sciences* 115, 2584–2589.
- Sugita, S., 1994. Pollen representation of vegetation in Quaternary sediments: Theory and method in patchy vegetation. *Journal of Ecology* 82, 881–887.
- Tang, H., Dubayah, R., Swatantran, A., Hofton, M., Sheldon, S., Clark, D.B., Blair, B., 2012. Retrieval of vertical LAI profiles over tropical rain forests using waveform lidar at La Selva, Costa Rica. *Remote Sensing of Environment* 124, 242–250.
- Tinner, W., Kaltenrieder, P., 2005. Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. *Journal of Ecology* 93, 936–947.
- Tomppo, E., Gschwantner, T., Lawrence, M., Mroberts, R.E., 2010. National Forest Inventories: pathways for common reporting. Springer Science + Business Media.
- Uene, Icp Forests Programme Co-Ordinating Centre, 2016. In: TIOF, Ecosystems (Ed.), *Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of pollution on forests*, Eberswalde.
- Urban, M.C., Bocedi, G., Hendry, A.P., et al., 2016. Improving the forecast for biodiversity under climate change. *Science* 353.
- Vaglio Laurin, G., Puletti, N., Chen, Q., Corona, P., Papale, D., Valentini, R., 2016. Above ground biomass and tree species richness estimation with airborne lidar in tropical Ghana forests. *International Journal of Applied Earth Observation and Geoinformation* 52, 371–379.
- Valladares, F., Matesanz, S., Guilhaumon, F., et al., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* 17, 1351–1364.
- Van Der Plas, F., Ratcliffe, S., Ruiz-Benito, P., et al., 2018. Continental mapping of forest ecosystem functions reveals widespread synergies. *Ecology Letters* 21, 31–42.
- Vayreda, J., Martínez-Vilalta, J., Gracia, M., Retana, J., 2012. Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. *Global Change Biology* 18, 1028–1041.
- Viellefont, G., Courbaud, B., Kunstler, G., Dhôte, J.-F., Clark, J.S., 2009. Biases in the estimation of size-dependent mortality models: advantages of a semiparametric approach. *Canadian Journal of Forest Research* 39, 1430–1443.

- Vilà-Cabrera, A., Martínez-Vilalta, J., Retana, J., 2015. Functional trait variation along environmental gradients in temperate and Mediterranean trees. *Global Ecology and Biogeography* 24, 1377–1389.
- Vizcaíno-Palmar, N., Benito-Garzón, M., Alía, R., et al., 2019. Geographic variation of tree height of three pine species (*Pinus nigra* Arn., *P. pinaster* Aiton and *P. pinea* L.) gathered from common gardens in Europe and North-Africa. *Annals of Forest Science* 76, 77.
- Wardle, D.A., Bardgett, R.D., Walker, L.R., Peltzer, D.A., Lagerstrom, A., 2008. The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences. *Oikos* 117, 93–103.
- White, J.C., Coops, N.C., Wulder, M.A., Vastaranta, M., Hilker, T., Tompalski, P., 2016. Remote Sensing Technologies for Enhancing Forest Inventories: A Review. *Canadian Journal of Remote Sensing* 42, 619–641.
- White, K., Pontius, J., Schaberg, P., 2014. Remote sensing of spring phenology in northeastern forests: A comparison of methods, field metrics and sources of uncertainty. *Remote Sensing of Environment* 148, 97–107.
- Williams, J.W., Grimm, E.C., Blois, J.L., et al., 2018. The Neotoma Paleocology Database, a multiproxy, international, community-curated data resource. *Quaternary Research* 89, 156–177.
- Wohlfahrt, G., Galvagno, M., 2017. Revisiting the choice of the driving temperature for eddy covariance CO<sub>2</sub> flux partitioning. *Agricultural and Forest Meteorology* 237–238, 135–142.
- Wu, B., Yu, B., Wu, Q., Huang, Y., Chen, Z., Wu, J., 2016. Individual tree crown delineation using localized contour tree method and airborne LiDAR data in coniferous forests. *International Journal of Applied Earth Observation and Geoinformation* 52, 82–94.
- Yang, W., Tan, B., Huang, D., et al., 2006. MODIS leaf area index products: from validation to algorithm improvement. *IEEE Transactions on Geoscience and Remote Sensing* 44, 1885–1898.
- Yu, X., Hyypä, J., Kaartinen, H., Maltamo, M., 2004. Automatic detection of harvested trees and determination of forest growth using airborne laser scanning. *Remote Sensing of Environment* 90, 451–462.
- Yu, X., Liang, X., Hyypä, J., Kankare, V., Vastaranta, M., Holopainen, M., 2013. Stem biomass estimation based on stem reconstruction from terrestrial laser scanning point clouds. *Remote Sensing Letters* 4, 344–353.
- Zanne, A.E., Tank, D.C., Cornwell, W.K., et al., 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506, 89.
- Zhao, K., Popescu, S., 2009. Lidar-based mapping of leaf area index and its use for validating GLOBECARBON satellite LAI product in a temperate forest of the southern USA. *Remote Sensing of Environment* 113, 1628–1645.
- Zianis, D., Muukkonen, P., Mäkipääand, R., Mencuccini, M., 2005. Biomass and Stem Volume Equations for Tree Species in Europe. In: Science TF50F (Ed.), *Silva Fennica*.
- Zolkos, S.G., Goetz, S.J., Dubayah, R., 2013. A meta-analysis of terrestrial aboveground biomass estimation using lidar remote sensing. *Remote Sens Environ* 128, 289–298.