Tree Genetics & Genomes (2020) 16:67
https://doi.org/10.1007/s11295-020-01451-1

REVIEW

# Integrating evolutionary, demographic and ecophysiological processes to predict the adaptive dynamics of forest tree populations under global change

**Sylvie Oddou-Muratorio**[1] · **Hendrik Davi**[1] · **François Lefèvre**[1]

Received: 29 November 2019 / Revised: 9 April 2020 / Accepted: 3 July 2020

## Abstract

Three types of process-based models (PBMs) are traditionally used to predict the response of forest tree populations to global change (GC): (i) ecophysiological models, which simulate carbon and water fluxes in forest ecosystems by explicitly integrating the effects of climate and $CO_2$; (ii) forest dynamics models which simulate forest successions by explicitly linking mortality, growth and regeneration processes; and (iii) evolutionary dynamics models, which simulate the variation and evolution of adaptive traits by explicitly accounting for selection, mutation, gene flow and inheritance rules. The ongoing context of rapid GC, however, questions the boundaries between these types of models. Here, we review different strategies of model integration: (i) physio-demographic PBMs, integrating physiological and demographic processes; (ii) demo-genetic PBMs, integrating demographic and evolutionary processes; and (iii) physio-demo-genetic PBMs, which attempt to integrate these three types of processes. We show that these integrative models allow a better understanding of how different functional traits influence demographic rates (the phenotype-demography map), how the variation in demographic rates influences fitness (the demography-fitness map) and how individual variations of fitness may in turn influence the genetic composition of a population. Our review highlights that accounting for inter-individual variation in ecological processes is increasingly recognized as crucial for modelling the ecosystem response to environmental change. We argue that the effort of integrating these different processes is valuable, both for a basic understanding of their interactive effects on the responses of forests to GC and for applied horizon scanning to support adaptive strategies.

**Keywords** Inter-individual variation · Process-based models · Demo-genetic models · Physio-demographic models · Physio-demo-genetic models · Intraspecific variation · Functional traits · Performance traits

## Introduction

Predicting the response of trees, the keystone species of forest ecosystems, to ongoing global change (GC) is a critical ecological, societal and economic issue. Indeed, forests provide a multiple source of ecosystem services and well-being to human populations, including biodiversity sustainability, carbon sequestration and freshwater availability. Observed and predicted impacts of GC on forest trees involve a wide variety of abiotic stresses (e.g. drought, wind throw, flood, heavy snow, late frosts, fire) and biotic stresses (predation, competition), which are driven by climate change. GC impacts also involve changes in forestry practices, deforestation, nitrogen deposition or pollution, land use changes and increasing opportunities for rapid pest expansion. In particular, increasing droughts have been associated with decreasing tree growth and forest productivity (Zhao and Running 2010), increased risks of tree mortality (Allen et al. 2010), higher fire frequency (Moriondo et al. 2006), and loss of ecosystem services (Anderegg et al. 2013). These negative effects of GC can also be mitigated by increasing length of vegetation period (Davi et al. 2006), increasing $CO_2$ concentrations (Davi et al. 2006; Gea-Izquierdo et al. 2017) and nitrogen fertilization (Quinn

---

Communicated by S.C. González-Martínez

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s11295-020-01451-1) contains supplementary material, which is available to authorized users.

✉ Sylvie Oddou-Muratorio
sylvie.muratorio@inrae.fr

[1] INRAE, UR 629 Ecologie des Forêts Méditerranéennes, URFM, 84000 Avignon, France

Thomas et al. 2010). All these changes interact in a complex way and are likely to result in new biotic and abiotic conditions, unobserved in the past.

Depending on their nature, frequency, duration, or intensity, environmental stresses will have various impacts on trees. These stresses can affect tree structure (e.g. branch mortality, leaf fall), seasonal physiology (e.g. growth cessation, reduced photosynthesis, hydraulic failure) and overall vigour (e.g. crown defoliation) and performances (e.g. reduced growth, reproduction and survival) up to the limits of their *phenotypic plasticity**.[1] At population level, these stresses also impose strong selective pressures, which affect demographic rates and can cause *genetic adaptation** across generations or cause population extinction. Moreover, at the ecosystem level, these stresses affect the ecological processes driving community composition depending on the variability of species' *resistance and resilience**. The interplay between phenotypic plasticity, genetic evolution, and community rearrangement ultimately determines the ability of populations and ecosystems to adjust to new environmental conditions imposed by GC.

Mechanistic, *process-based models** (PBMs) have attracted an increasing interest in ecology, considering their ability to predict possible future dynamics of ecological systems by accounting for the variety and complexity of environmental changes and their impacts (Jeltsch et al. 2008; Evans 2012; Mouquet et al. 2015; Maris et al. 2018). Three types of PBMs are traditionally used to predict the response of forests to GC (Box 1, Fig. 1): (i) *ecophysiological models*, which simulate carbon and water fluxes in forest ecosystems by explicitly integrating the effects of climate change, nitrogen deposition and $CO_2$ fertilization; (ii) *forest dynamics models* which simulate changes of forest structure and successions in response to disturbances and management by explicitly linking mortality, growth and regeneration processes; and (iii) *evolutionary dynamics models*, which simulate the evolution of adaptive traits and genetic diversity in response to explicit mutation, selection and gene flow processes, while genetic drift dynamically results from demographic processes.

The ongoing context of rapid GC, however, questions the boundaries between these different PBMs. On the one hand, evolutionary ecologists increasingly realized that new insight on evolutionary dynamics can be obtained by incorporating more details on the demographic dynamics and the ecological and environmental context into population genetics and quantitative genetics models (Hanski 2012; Hendry 2016). In particular, in non-stationary systems where the evolutionary drivers themselves have their own dynamics, a mechanistic approach is required to build up the *fitness** response to environmental changes. On the other hand, ecophysiologists and population ecologists have also become increasingly aware that the widespread variability that exists among individuals for *functional** and *life-history traits** can no longer be ignored to predict ecosystem carbon fluxes and stocks, or population dynamics (Moran et al. 2016). Indeed, the genetic composition of a population, which determines much of its phenotypic variation, and its *evolutionary dynamics** may both affect population dynamics or ecosystem-level carbon and water fluxes. This contradicts a common expectation that changes in the genetic composition of a population (particularly in long-lived organisms) occur so slowly that the physiological responses to environment, the demographic dynamics and the evolutionary dynamics, remain decoupled from each other. However, an increasing number of studies are challenging this expectation and suggest that when selection is strong, i.e. when the environment changes substantially and rapidly, these physiological, demographic and evolutionary dynamics can occur on the ecological timescale (Pelletier et al. 2007).

In such situations, integrating physiological, demographic and/or evolutionary processes into a new PBM (integrative PBM in the following) may be more appropriate than keeping either a demographic-oriented, physiological-oriented or evolutionary-oriented approach. However, this may come at the cost of increasing model complexity, a notion which has been thoroughly discussed elsewhere (e.g. Evans et al. 2013; Getz et al. 2018; Maris et al. 2018). Getz et al. (2018) underline that to answer the plurality of scientific issues in ecology, we need a plurality of PBMs involving different hierarchical levels of ecological systems and different processes. Their typology of ecological model in terms of their structural, process, and utility complexity also suggests that integrative PBMs are bound to be more complex in terms of processes and structure than the ecophysiological, forest dynamic or evolutionary dynamics models they inherit from. However, such increasing model complexity may be desirable (Evans et al. 2013), and the distinction made by Maris et al. (2018) between complicatedness and complexity is helpful to justify this point of view. Indeed, integrative PBMs may be more complex not only because they are more complicated (e.g. more processes, more hierarchical levels) but also because they attempt to capture the complexity per se of ecological systems, i.e. the emergence of new features (such as fitness) from the combination of their subcomponents.

This review investigates how PBMs integrating the processes involved in the physiological responses to the environment, the demographic dynamics and the evolutionary dynamics contribute to a better prediction of the eco-evolutionary dynamics of forests under GC. We define and review (1) physio-demographic PBMs, integrating physiological and demographic processes; (2) demo-genetic PBMs, integrating demographic and evolutionary processes; and (3) physio-demo-genetic PBMs, which attempt to integrate these three types of processes. For each of these three levels of integration, we highlight the focal emergent property(ies) that can be captured, the scientific

---

[1] Terms in italic with an asterisk (*) are defined in the glossary.

## Box 1: Three main bricks to build up integrative eco-evolutionary, process-based models

**Ecophysiological models** simulate biogeochemical cycles between the canopy, the atmosphere and the soil by linking together the physical and physiological processes such as radiative transfer, evapotranspiration, photosynthesis, respiration or carbon allocation. A large number of ecophysiological PBMs exist and differ primarily from each other in the resolution at which vegetation is abstracted. Dynamic Global Vegetation Models (DGVMs) aggregate individual tree, grass, and shrub species into generic plant functional types (PFTs) to simulate the vegetation distribution at global or continental scales. DGVMs focus on the ecological processes and disturbances that determine the balance between PFTs, such as establishment, competition, growth and mortality, and allow vegetation, soil moisture, and nutrient availability to respond to atmospheric forcing and land management changes (Cramer et al. 2001). Other models use an explicit representation of single species' physiology to simulate vegetation functioning at a finer spatial scale (e.g. Simioni et al. 2000; Ogée et al. 2003; Misson et al. 2004; Dufrêne et al. 2005; Briceno-Elizondo et al. 2006). These later models can (but not necessarily do) account for more detailed ecophysiological processes, for instance by representing stand vertical structure and competition for light (Simioni et al. 2000). The grouping of single tree species into PFTs has been shown to be a successful approach to reduce complexity in ecophysiological models (Fischer et al. 2016), and the predictions of DGVM are usually quite robust to spatial resolution. The main properties of ecophysiological PBMs are first that they simulate vegetation functioning in response to *explicit climate and soil variability* (as input variables), through their impacts on plant/PFTs physiology. They are also usually completely *deterministic:* the simulated response of a given system to a given climate and environment will always be the same.

**Forest dynamics models,** initially devoted to the prediction of yield and growth in response to management practices, have rapidly incorporated the effects of mortality, growth and reproduction in a more general approach of plant population dynamics (Jeltsch et al. 2008). In gap models, a first generation of individual-based models (IBM) for forest dynamics, the mortality of a large and dominating tree, resulting either from management, e.g. thinning and logging, and/or natural disturbance, produces gaps in the forest, which leads to the release of suppressed trees and increased tree recruitment rates (Bugmann 2001). Then, the establishment, growth and mortality of individual trees on small patches of land are simulated as a function of biotic (competition) and abiotic factors (climate and soil). Cellular automata models are another approach to tackle specific spatial issues related to interactions between neighbours which were used in forest dynamics models (Grimm et al. 2005). Different improvements now allow multispecies forest dynamics models to simulate forest successions and species diversity by accounting for the effects of dispersal, landscape heterogeneity and disturbances (e.g. Lischke et al. 2006; Seidl et al. 2012). In general, forest dynamics PBMs are *individual-based* and model forest dynamics as an emergent property of interactions and feedbacks between the adaptive agents of a complex system, i.e., individual trees, and their environment. As compared to ecophysiological PBMs, they incorporate some *stochastic* processes (e.g. related to dispersal) together with *deterministic* ones. They also model more *implicitly* the impact of drivers such as climate on forest dynamics, but allow the widest variety of drivers to be incorporated (e.g., biotic drivers related to pests).

**Evolutionary dynamics models** are concerned with the variation and evolution of heritable traits that have a direct effect on **fitness***. Among the more common formalisms of evolutionary change are (1) population genetics, which model the evolution of gene frequencies at the expense of ecological detail; (2) quantitative genetics, which integrate the genotype-phenotype map; (3) evolutionary game theory, which incorporates ecological realism, in particular the notion that the success of any given strategy depends on its frequency within the population, but often ignores genetic detail. Such evolutionary dynamics models aim to understand the long term destiny of new mutations that affect the phenotype given the variability present in the population. Based on the infinitesimal model of quantitative genetics and benefitting from the development of high throughput genomic data and analytical tools, population genetics and quantitative genetics approaches are on a converging trajectory (Nelson et al. 2013). We focus here on quantitative genetics PBMs, which simulate how selection, mutation, gene flow and genetic drift interact to shape the evolution of adaptive traits and of population demography, by explicitly accounting for the mechanisms underlying the inheritance of the adaptive traits. While theoretical, analytical quantitative genetic models are *deterministic*, simulation IBMs allow some *stochastic* processes to be included (e.g. related to mating system, dispersal). As compared to ecophysiological and forest dynamics models, the response to environmental drivers is much more *abstracted*, e.g. an optimal phenotypic value is usually considered to maximize individual fitness in a given environment, and this phenotype-fitness relationship is assumed to be fixed.

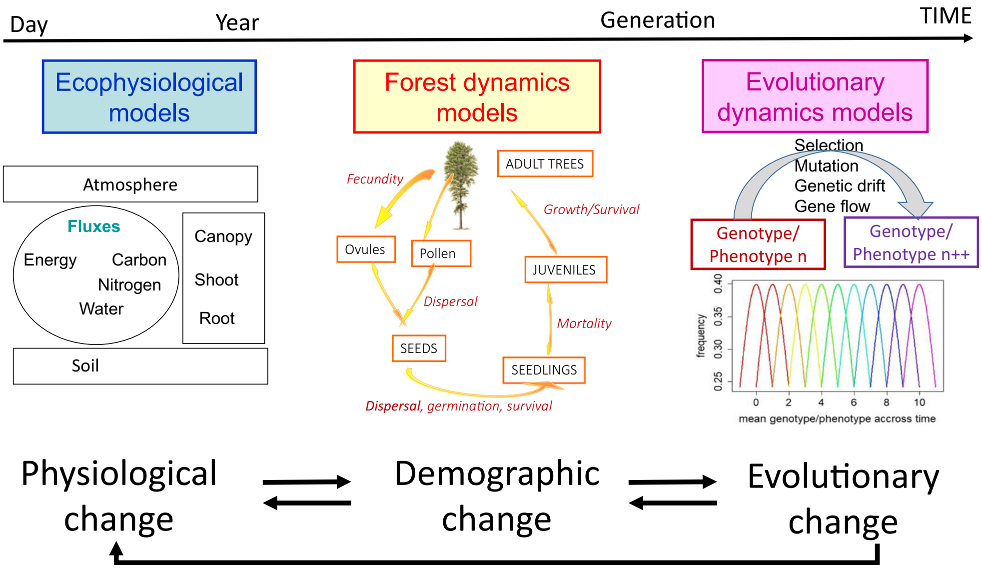


**Fig. 1** The different PBMs used to investigate physiological, demographic and evolutionary changes in tree populations and their coupling. See Box 1 for a description of each model. Several types of coupling between physiological responses to environment, the demographic dynamics and the evolutionary dynamics are possible: physiological change may influence demographic change (e.g. when carbon starvation or hydraulic failure in response to repeated or severe droughts induce tree mortality), while demographic change may influence physiological change (e.g. when tree mortality reduces local competition for water). Demographic change obviously affects evolutionary change (as variation in survival and reproduction drives fitness and the process of selection), while evolutionary change can influence demographic change (e.g. selection for earlier reproduction will affect the dynamics of regeneration). The effect of physiological change on evolutionary change operates through demographic change, but evolutionary change can influence physiological change more directly (e.g. when drought-resistant genotypes are selected). Most importantly, there may also be reciprocal effects (e.g. feedback loops) between physiological, demographic and evolutionary change, and this paper is particularly concerned with them

challenges and the challenges related to data sources for the evaluation of models. Finally, in the last section (‘Roadmap’), we discuss which processes should be integrated depending on the focal issue, which spatial and temporal resolution of inter-individual variation (iVa) is required and how processes can be integrated while limiting model complexity and challenges related to data-model linkage.

## Definitions and methods

### Definition of the considered integrative models

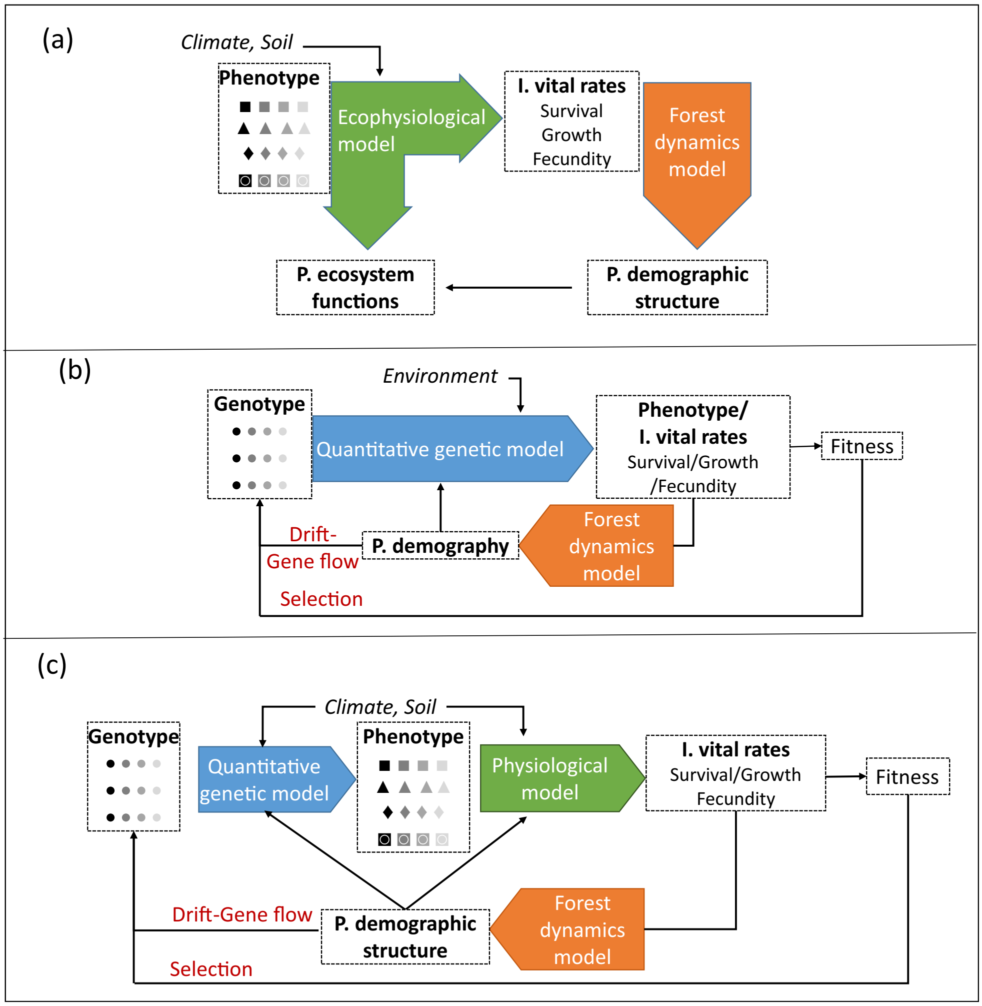
We followed the *genotype-phenotype-fitness map*'s* framework proposed by Coulson et al. (2006) to propose theoretical definitions of the three integrative PBMs considered in this review.

**Physio-demographic models** These PBMs include a *phenotype-demography map**, modelling how different functional traits contribute to the demographic rates (Fig. 2a). This map allows population demography and ecosystem functions to emerge from physiological processes. Although fitness does not explicitly appear on this framework, fitness' components (survival, reproduction) do and determine the demographic structure. Hence, the main value of physio-demographic models is to analyse how different values and combinations of functional traits contribute to fitness. Note that physio-demographic models are not necessary individual-based models (IBMs), as functional traits may be modelled at cohort or population level.

**Demo-genetic models** These IBMs integrate a *genotype-phenotype map**, restricted to life-history traits, with *phenotype-demography* and *demography-fitness maps** (Fig. 2b). This integration allows iVa in fitness and hence opportunities for selection to emerge from demography, which in turn affects the genetic composition of the population over successive generations (feedback loop). Hence, in contrast to theoretical models that usually consider the speciation timescale, a main value of demo-genetic models is their capacity to examine fitness evolution at a contemporary, ecological timescale (few generations), including transient dynamics out of equilibrium (Coulson et al. 2006). Moreover, demo-genetics models are particularly suitable in highlighting the building up of fitness in natural populations, as those traits promoting survival and offspring production are demographically favoured.

**Physio-demo-genetic models** These IBMs integrate a *genotype-phenotype map*, focussed on functional traits, with

**Fig. 2** Conceptual framework for the coupling of demographic, physiological and/or evolutionary processes in (**a**) physio-demographic models (**b**) demo-genetic models and (**c**) physio-demo-genetic models. Squared, white boxes represent dynamic state variables of the system; while coloured, arrow-shaped boxes represent the different models used to simulate them. Black italic text represents the forcing variables related to the environment. Red text represents the evolutionary processes. I stands for individual and P for population. In the Genotype box, each line represents a locus, the different shades of grey indicating different alleles. In the Phenotype box, each line represents a functional trait, the different shades of grey indicating different trait values



*phenotype-demography* and *demography-fitness maps** similar to physio-demographic models. They include the feedback effect of population demography on its genetic composition at next generation, as in demo-genetic models (Fig. 2c). Specifically, physio-demo-genetic models allow dynamic changes of iVa in physiological parameters to emerge from both environmental changes, including those due to changes in stand structure, and genetic changes, thus closing the full physio-demo-genetic loop.

Note that all of the physiological, demographic or evolutionary processes are not necessarily included in each of these integrative PBMs. Still, because we focus here on the building up of fitness through the physiological or demographic response to environmental variation, we chose to consider only PBMs integrating at least some demographic processes. Moreover, we argue that IBMs are best suited to integrate the components of fitness related to interactions among individuals (e.g. competition, facilitation, reproduction through pollen dispersal), which are essentially demographic. Hence, we do not address here the integration of physiological and genetic processes without demography.

## Literature search

Literature search was conducted using the Web of Science (WoS) over the period from January 1, 1992, to December 31, 2018.

**Physio-demographic models** We searched in the WoS for papers that had addressed joint modelling of the forest functioning and the processes involved in forest dynamics. Research terms were (forest AND tree AND (physiolog* OR vegetation) AND (mortality OR survival OR growth OR dynamic*) AND (process-based model* OR DGVM* OR DVM*). We identified 276 references. The number of papers per year strongly increased over the period, following the increase in the global number of publications on models in ecology. We analysed the summaries of each article to eliminate synthesis papers and those that did not present model results. We kept 92 references (Online Supplementary Table S1).

**Demo-genetic models** We searched for forest models integrating demographic processes and genetic variation. We used a first query based on the following terms: (forest*) AND (metapop* OR demogr*) AND (variability OR diversity) AND (model) AND (simul*). This search provided 169 references over the period from January 1, 1992, to December 31, 2018. We removed review papers and publications that did not relate to trees, or used models for inference rather than for predictions, or had no demographic processes, or made no link between variation and demography, and we finally kept 19 publications from this list. We did a second query based on the following terms: (forest*) AND (population viability analysis OR population size) AND (simul*) AND (adapt* OR evolut* OR genet*). This query provided 238 publications from which we filtered eight that were additional to the previous list. Then we used a third query: (forest dynamics*) AND (metapop* OR demogr*) AND (model*) AND (adapt* OR evolut* OR genet*), which provided two additional references. Finally, we identified another set of six publications from the literature cited in the previous references, which gave a total of 35 references. For each publication, we characterized the resolution of inter-individual variability and its genetic make-up, the demographic processes, the coupling between variability and processes, and their spatio-temporal scales (Online Supplementary Table S2).

**Physio-demo-genetic models** Research terms were as follows: (demogr* OR dynamic* OR mortality OR survival OR growth) AND (adapt* OR evolut* OR genet* OR genot*) and (dynam* OR variat*)) AND (physiol* OR ecophysiol* OR vegetation OR (functional trait*)) AND (model* OR simulat* OR DGVM* OR DVM*) AND (process-based OR individual-based OR IBM OR mechanist*) AND forest* AND tree*. After checking, we identified only eight original research articles (Online Supplementary Table S3).

## Integrating demographic and physiological processes

### State of the art

In general, ecophysiological models have not been specifically developed to consider the key demographic processes shaping population dynamics, which quickly came to be seen as presenting a large source of uncertainty in their predictions (Fisher et al. 2010). Hence, accounting for demographic processes such as growth, reproduction, seed dispersal, seedling recruitment, and tree mortality is now acknowledged as a major prerequisite to predict carbon and water fluxes over long periods of time. Simultaneously, the incorporation of changing environmental conditions has become a priority in forest dynamics models, in order to address such issues as how changes in forest community structure may mitigate the effect of GC.

**Ecophysiological models integrating demography** A first strong motivation to account better for demographic processes in ecophysiological models arose from the need to study the impact of forest management on the carbon cycle (Landsberg and Waring 1997). Moreover, tree size measurements (i.e. diameter or height increment) are available in great quantities in forest inventories and have been used to validate the predictions of ecophysiological models. For these two main reasons, tree growth has been the first major process of forest dynamics incorporated into dynamic vegetation models (DVMs). Most of the existing stand-scale ecophysiological models are now able to consider the effects on stand growth of both GC and changes in stand structure. This integration of physiological and dynamic processes has enabled the assessment of the impact of forest management on the carbon cycle, both on local and global scales (Briceno-Elizondo et al. 2006; Fujii et al. 2009; Bellassen et al. 2010). For instance, using the dynamic global vegetation model (DGVM) ORCHIDEE-FM, Bellassen et al. (2010) found that the $CO_2$ net ecosystem exchange of unmanaged forests is 40% lower than that of managed forests and concluded that management explains 40% of the accumulated carbon sink over 150 years. However, discrepancies between the net ecosystem production, simulated by ecophysiological models, and growth, measured in inventories, are still often reported (Babst et al. 2013) and call for the improvement of carbon allocation modelling (Buckley and Roberts 2006).

The study of climate-related mortality has also promoted the integration of ecophysiological and demographic processes. In the current context of increasing drought intensity and duration (Adams et al. 2017), ecophysiological models allow a fine description of the processes underlying drought-induced tree decline and mortality, e.g. hydraulic failure and/or carbon starvation (although the two processes are seldom simultaneously accounted for in the same model). Therefore, they complement forest dynamics models, which have traditionally focused on regular mortality due to competition (Hulsmann et al. 2018). Taking into account the mortality due to drought or high temperatures induces significant changes in vegetation in DGVM simulations (Jiang et al. 2012). For instance, Collalti et al. (2019) found that the combined impacts of climate change and changing $CO_2$ concentrations lead forests to grow faster, mature earlier and die younger. However, they also found that under future climate conditions, forest thinning could reduce the climate-induced risks of mortality (Halofsky et al. 2018).

Compared to growth and mortality, reproduction is the demographic rate that has received the lowest consideration in ecophysiological models (Vacchiano et al. 2018). Almost no DVMs clearly assess the detailed investment in reproduction, nor validate (pollen and) seed production model with data, and very few papers evaluate the regeneration module of their model even when this component is detailed (e.g. Ditzer et al. 2000). However, this field of research is rapidly evolving, and approaches investigating the relationships between physiological processes and demographic rates are currently developed (Poorter et al. 2008; Visser et al. 2016; Bontemps et al. 2017). While most models simulate regeneration, the effect of climate change on this component is rarely studied and models are poorly evaluated on this aspect.

Finally, as DGVMs aim to integrate the ecological processes and disturbances that determine the distribution of plant functional types (PFTs) at global scale, they can be considered as a first attempt to map physiological processes onto population demography (as summarized by survival) at the coarse scale of species/biome distribution (Cheaib et al. 2012; Case and Lawler 2017). At this global scale, other PBMs integrate a functional approach of species fitness. In particular, the PHENOFIT model computes the probability of presence for an individual over several years, estimated by the product of the survival probability until the next reproductive season, and the probability of producing viable seeds by the end of the annual cycle (Chuine and Beaubien 2001).

**Forest dynamics models integrating ecophysiology** At stand scale, an alternative approach is to include ecophysiological processes in forest dynamics models (Pitelka et al. 2001). Forest dynamics models were originally conceived to study how vegetation structure and composition change over time under current climatic conditions, considering abiotic and biotic constraints to establishment, growth and survival. A first way to account for climate change in forest dynamics was to couple gap models with models accounting for soil carbon/nitrogen turnover and the dynamics of abiotic environment (e.g. climate) with further details. The main objective of these hybrid models was to include not only a minimum number of ecological assumptions but also robust parameterizations of the effects of climate on plant population dynamics (Bugmann 1996). This was done by defining the simplified niche for each species (e.g. three-dimensional: temperature, moisture and light) and by accounting explicitly for environmental effects on establishment, growth and survival. For instance, the number of recruited trees, which usually depends on species' shade tolerance, was modelled as depending also on another's niche's dimensions. Diameter growth was usually modelled as a deterministic process, considering that the potential (i.e. maximum possible) growth is reduced by scalars that represent the extent of suboptimal conditions due to abiotic stress or competition. Talkkari et al. (1999) showed how gap model predictions could be improved by refining the growth response curve to temperature. Taking into account the inter-annual variations in growth in response to drought also significantly improved gap models (Mina et al. 2016). Another ongoing major development of gap models is to improve the modelling of mortality, by better accounting for stress-related mortality together with background mortality.

These hybrid models were used to examine the relationships between ecosystem functioning and community dynamics. Ditzer et al. (2000) showed that the biomass of a Malaysian tropical forest succession stabilized after 100 years. Chauvet et al. (2017) confirmed the expected decrease in species richness with decreasing site fertility. These models were also used to investigate how forest management affects community composition (Kammesheidt et al. 2002; Fujii et al. 2009). Finally, these models were also compared to niche models for their ability to predict species distribution (Gutierrez et al. 2016).

**Conclusion** Our literature review highlights that over the last few decades, ecophysiological models and forest dynamics models have been on a converging trajectory (as denoted by the generic term DVM increasingly used for both categories of models). Forest dynamics models are increasingly integrating ecophysiology (19% out of 92 references) while ecosystem functioning models are increasingly integrating demographic processes (79%), with some fully integrative approaches (2%). These models are used either at a global scale (42%) or at the scale of regions (12%) or plots (46%), by taking into account the specificities of species or sites.

## Scientific challenges

The ongoing integration of ecophysiological and forest dynamics models into physio-demographic PBMs (also called hybrid DVMs) allows more accurate predictions of forest dynamics under climate and GC. The main challenges for physio-demographic PBMs lie in the limited knowledge on the physiological processes determining demographic rates and on their interactions. In particular, reproduction is still a black box. There is still limited knowledge on the age of first reproduction, which affects the overall fecundity of a tree and which is determined both by the abiotic environment (e.g. climate) and by stand and tree characteristics (e.g. height, growth and light availability mediated by competition). Carbon allocation to the initiation and maturation of pollen and seeds also remains largely unknown. As resources allocated to reproduction cannot be used for other functions, trade-offs may occur for instance between fecundity and growth, particularly under stressful conditions (Obeso 1988). Finally, tree fecundity alone is not enough to predict regeneration, the ultimate reproductive success of a tree depending on other processes affecting mating probability (pollen quantity and quality, pollen dispersal), seed germination (including inbreeding depression) and seedling survival (Oddou-Muratorio et al. 2018). The physiological determinants of these processes remain largely ignored in ecophysiological models, hindering the prediction of CC effects over the whole tree life cycle.

Although physio-demographic PBMs account better for the physiological processes driving tree growth, the integration between stand structure and tree physiology ideally requires explicit 3D modelling of tree functioning including its architecture, which is computationally costly (Marie and Simioni 2014). More generally, carbon allocation to root and carbohydrates reserves remains largely unknown and calls for the development of more mechanistic allocation models accounting for the dynamics of each sink such as wood, leaves or roots (Guillemot et al. 2015). The modelling of reserves is also a major research topic (Fang et al. 2019), as it determines the probability of mortality and the resilience of trees after disturbances such as drought or insect attacks. The physiological causes of mortality are still a matter of scientific debate, as a single factor (e.g. drought) associated with massive mortality may involve several underlying physiological processes, with several mortality thresholds, and potential feedback between them (McDowell et al. 2013, 2016; Davi and Cailleret 2017). Even though hydraulic failure is increasingly acknowledged as the initial step triggering a number of interacting processes leading to mortality (Adams et al. 2017), the relationships between carbon and water fluxes, and the role of biotic factors during and after drought, remain to be clarified. Physio-demographic PBMs are useful tools to investigate these issues because of their ability to predict the physiological thresholds of key functional traits triggering mortality (Davi and Cailleret 2017).

### Data source challenges

One of the major shortcomings of physio-demographic PBMs is the large number of parameters of ecophysiological PBMs (e.g. around 78 species-specific parameters and 12 site-specific parameters in CASTANEA; Dufrêne et al. 2005). These parameters usually have a physical or physiological significance and can be independently estimated empirically. The parameterization and evaluation of these models has always been a central issue (Davi et al. 2006), but it becomes an obstacle to using these models on a large number of species when taking into account the iVa of multiple parameters.

Fortunately, the increase in data acquisition capacity and the obligation to share these data open new perspectives (Table 1). One of the difficulties is that available databases on physiological traits have been constituted by different scientific communities, except the TRY database that assembles performance and functional traits data (https://www.try-db.org/; Kattge et al. 2020). The data are therefore often heterogeneous with varying access rights. Another general problem is that data sources often relate to traits that differ from model parameters (for instance, budburst date is measured while model parameters relate to the sum of temperature required for reaching a certain state). Sometimes the data coincide with parameters, but their units differ. In addition, some physiological traits are not yet systematically measured, such as those determining respiration or the optical properties of leaves and needles. Finally, a safe use of these data often requires expert knowledge.

## Integrating demographic and evolutionary processes

### State of the art

The idea that demographic rates, such as fecundity and the probability of mortality, vary among individuals partly for genetic reasons, and thus that the genetic composition of a population and its evolutionary dynamics can influence the demographic dynamics, has been incorporated for decades in evolutionary quantitative genetics theory (Hanski 2012; Hendry 2016). However, the development of fully integrative forest demo-genetic models has lagged behind, as illustrated by the only 35 publications found on forest demo-genetic models. We categorized these publications into three categories, as described in the following sections.

**Population genetics models integrating demography** Le Corre et al. (1997), Austerlitz et al. (2000) and Austerlitz and Garnier-Géré (2003) used metapopulation models to demonstrate how specific demographic features of trees, e.g. long-distance dispersal and juvenile phase, can explain their high level of genetic diversity compared to other organisms. Leslie matrix models, forest growth models or IBMs may explicitly account for forest dynamics processes such as growth/competition balance, seed dispersal and mortality. Integrating sexual reproduction processes (gametogenesis and fecundation) into such models, several studies have shown how tree demography and silviculture can shape the amount and structure of neutral genetic diversity at single-population scale (Degen et al. 1996; Degen et al. 2006; Sebbenn et al. 2008; De Lacerda et al. 2013; Vinson et al. 2015). Wernsdörfer et al. (2011) integrated neutral genetic diversity in a forest gap model with detailed demographic processes, including multiple life-stage mortality processes and interspecific competition, to study the interaction of dispersal and demography on the preservation of neutral genetic diversity. Similar approaches were used to analyse the impact of biological drivers, such as animal pollination (Degen and Roubik 2004) or clonality (Jolivet and Degen 2011), and anthropogenic practices, such as deforestation (Kashimshetty et al. 2015) on neutral genetic diversity. Kuparinen et al. (2010) developed a demo-genetic model with variable mortality rate and showed the beneficial role of mortality on the rate of adaptation. In all these models, demography is the driver and genetic diversity is the target, whether it be neutral or under selection, but there is no feedback effect of genetic changes altering the demographic processes themselves.

**Table 1** List of databases (DB) and variables available to parameterize (‘P’ column) or validate (‘V’ column) models

| Name of database (DB) | Variables | P | V | Reference |
|---|---|---|---|---|
| DBs for traits values | | | | |
| TRY | LMA, N, Seed mass, Vcmax, Vjmax | X | | Kattge et al. 2020 |
| A Global Data Set of Leaf Photosynthetic Rates, Leaf N and P, and Specific Leaf Area | Vmax, Vjmax, N | X | | Walker et al. 2014 |
| GlobAllomeTree | Biomass, dbh, height | X | | Henry et al. 2013 |
| NSCdata | NSC | X | X | Martínez-Vilalta et al. 2016 |
| GlobResp | R15, Q10 | X | | Atkin et al. 2015 |
| Sur-Eau | P50, Pgs90, Ptlp | X | | Martin-StPaul et al. 2017 |
| FLUXNET_2015 | GPP, Reco, NEE, ETR, Rn | | X | Pastorello et al. 2017 |
| The International Tree-Ring Data Bank | Ring width increment | | X | Zhao et al. 2019 |
| DBs for quantitative genetic parameters (heritability, coefficient of variation…) | | | | |
| Gene2Trait | NA[a] | X | | Kramer et al. unpublished data, Trees4Future EU project http://www.trees4future.eu/database-access.html |
| Deliverable D1.2 of NOVELTREE (FP7 EU project) | D13C, dbh, height, WD, SpG, LiC, architecture traits, resistance to pests | X | | Climent et al., unpublished data, Deliverable D1.2 of NOVELTREE EU project[b] |
| H2DB | dbh, height, WD, architecture traits | X | | Kaminuma et al. 2013 |

*LMA* leaf mass per area of leaves or needle, *N* nitrogen content of organs, *Vcmax* maximum rate of carboxylation, *Vjmax* maximum rate of electron transport, *dbh* diameter at breast height, *NSC* non-structural carbon content, *R15* respiration rate at 15 °C, *Q10* rate of change of respiration when increasing the temperature by 10 °C, *P50* leaf water potential that causes a decline of 50% in hydraulic conductance, *Pgs90* value of water potential causing 90% stomatal closure, *Ptlp* turgor loss point, *GPP* gross primary production, *Reco* ecosystem respiration, *NEE* net ecosystem exchange, *ETR* evapotranspiration, *Rn* net radiation, *D13C* ratio of carbon discrimination, *WD* wood density, *SpG* spiral grain, *LiC* lignin content

[a] This DB is available from its curator (K. Kramer)

[b] This DB is available from its author (J. Climent)

**Forest dynamics models integrating phenotypic variation** Another scientific community has developed models where some level of phenotypic, and therefore genetic, variation interferes with forest dynamics processes, but with no process of heredity: these are the multi-species forest community models, either at single community or at metacommunity scale. Here, we do not provide a systematic review of such models (see Porté and Bartelink 2002; Pretzsch et al. 2015), but we highlight how they achieve the integration of phenotypic diversity and dynamics. Chave and Norden (2007) developed a neutral metacommunity model to study the conditions for maintenance of tree species diversity at global level despite local demographic incidents and fragmentation. Takeuchi and Innan (2015) used a niche-structured local community model to evaluate the impact of niche differentiation among species on species abundance distributions as compared to a neutral model. Forest community models can also use precise characterization of the adaptive differentiation between species, either by considering variation in demographic rates (Kohyama 1994; Favrichon 1997; Scheller et al. 2005), variation among functional groups (Mailly et al. 2000; Boulangeat et al. 2014; Lasky et al. 2014), or combining both types of variation (Kohyama 2006). Jansen et al. (2012) used an age- and size-dependent integral projection model with categorized individuals to study the persistence of within-species iVa in growth performance and its demographic consequences, but this model did not include heredity or evolutionary mechanisms. Zuidema and Franco (2001) showed the importance to consider demographic rate variability in matrix population models, but their statistical approach does not consider iVa as a target parameter of interest as such.

**Demo-genetic models integrating demographic and evolutionary processes** Forest models that effectively account for interference between demographic processes and trait variation under genetic control are still scarce. Hoebee et al. (2008) and Broadhurst et al. (2008) used a spatially explicit

IBM, coupling demography and genetic variation for self-incompatibility (thus interfering with reproduction), to study small population viability in a shrub and tree species. Kuparinen and Schurr (2007) and, later on, DiFazio et al. (2012) studied transgene dispersal capacity in a forestry landscape by using spatially explicit IBMs with differential demographic rates for transgenic and normal trees (seedling establishment probability, growth, reproduction and mortality). Using a metapopulation model along an environmental gradient, Soularue and Kremer (2012, 2014) showed that different genetic clines result from the combination of assortative mating and selection. Moran and Ormond (2015) developed a niche-structured forest dynamics model for two ecotypes having different demographic rates with monogenic inheritance. Forest demo-genetic models that integrate quantitative genetic inheritance in demographic rates are still missing.

**Conclusion** Integration of forest dynamics and quantitative genetic models allows joint simulation of ecological and evolutionary dynamics. Dunlop et al. (2009) called eco-genetic modelling their approach to study the rate of multi-trait evolution by including genetic details and demographic/ecological feedback. Our literature review shows that eco- or demo-genetic models are not used very much yet in the forestry domain, though in other domains (e.g. fish population dynamics), they have shown their usefulness in generating testable predictions on evolutionary dynamics and evaluating alternative management strategies (Dunlop et al. 2009; Piou and Prévost 2013).

## Scientific challenges

The main challenge is to favour the development of these demo-genetic models in the forestry domain, considering their suitability to examine fitness evolution at a contemporary, ecological timescale (few generations), and to highlight the building up of fitness as resulting from demo-genetic feedback. Evolutionary quantitative gene models traditionally assume a fixed relation between traits and fitness (e.g. Le Corre and Kremer 2012). This fixed relationship is not a suitable hypothesis under GC. Some authors have proposed modelling climatic change as a temporal change in phenotypic optimum (Polechová et al. 2009), but such an approach does not account for the change in the intensity and type of selection related to the forest dynamics itself. By contrast, demo-genetic models account for a feedback loop where (1) the genetic diversity and its organization determines the demographic structure and population dynamics and (2) the demographic structure and population dynamics drive genetic drift, selection and gene flow, which in turn determine genetic diversity and its organization. They do not assume any fitness function a priori, but instead allow fitness to emerge as a consequence of the underlying population dynamics, through the integration of the *genotype-phenotype**, the *phenotype-demography** and the *demography-fitness maps**. The flexibility of these maps makes demo-genetic models suitable for a dynamic approach to ongoing evolution. The genotype-phenotype map is determined by the factors and relations specified in the model, and it is dynamically influenced by the local demographic structure acting as an environmental factor (e.g. a good genotype for reproduction will express differently in stands of high or low density). The phenotype-demography map directly emerges from the forest dynamics model and it is dynamically influenced by the population structure and the current diversity (i.e. a good genotype for reproduction will have a low reproductive success if suppressed by competition with dominant trees).

## Data source challenges

A major challenge to developing demo-genetic models is to integrate heritable iVa for demographic rates in the population dynamics model. The main difficulty is finding data sources to estimate quantitative genetic parameters for performances, in particular reproduction and survival: genetic variances and correlations, age effects, as well as environmental impacts of local stand structure (which will dynamically change in the model). The data may come from controlled experiments, but controlled experiments in genetics often do not explore the range of environmental conditions effectively found in a forest and are often limited to juvenile trees, whereas controlled experiments in silviculture often do not explore the range of genotypes. Alternatively, the data may come from in situ approaches. Quantitative genetic parameters, such as trait heritability, can be estimated from pedigree or parentage analysis combined with spatial statistics (Coltman 2005; Pemberton 2008). Pollen and seed dispersal functions as well as individual fecundities can be jointly estimated from inverse modelling approaches (Oddou-Muratorio et al. 2018). Once quantitative genetic parameter estimates are available for the target tree population, a virtual QTL decomposition approach is an efficient way to simulate individual tree genotypes given the quantitative genetic parameters not requiring more genomic knowledge than the level of ploidy (Bost et al. 2001). There is no major difficulty in integrating the rules that determine the genotype-phenotype map in spatially explicit individual-based forest dynamics models. The rules that determine the phenotype-demography map, e.g. the effective reproductive success along the whole life of an individual, directly emerge from the forest dynamics model with no other specific need.

## Integrating physiological, demographic and evolutionary processes

### State of the art

The synthesis between demo-genetic and physio-demographic models has given rise to physio-demo-genetic models, which allow individual variations in fitness and hence opportunities for selection to emerge from physiologically driven demography and genetic change in physiological parameters to be simulated across generations.

In a pioneer study, Kramer et al. (2008) coupled an ecophysiological model with a quantitative genetic model to investigate the potential of adaptive response of a beech stand for different traits (budburst phenology, spiral grain, height growth), driven by explicit climatic variation. Kramer and Van der Werf (2010) further underlined the power of such models to predict consequences of ongoing CC and forest management, e.g. non-stationary environments, on the functioning and genetic composition of tree populations.

Oddou-Muratorio and Davi (2014) used a similar integrative physio-demo-genetics model to examine the microevolution in the timing of budburst (TBB) along an altitudinal gradient of European beech. Simulations showed that five generations were sufficient to develop non-monotonic genetic differentiation in TBB along the local climatic gradient. In another study along a latitudinal gradient of European beech, Kramer et al. (2015) considered a two-phase model of budburst phenology within a physio-demo-genetics model and showed that the model reproduces patterns of genetic differentiation in TBB observed in natural populations.

While these first approaches rely on quantitative genetics to model the genetic architecture of adaptive traits, other approaches use game theory coupled with an ecophysiological model to identify evolutionary stable strategies (ESS) for major functional traits at community level. Dybzinski et al. (2011) first proposed an analytical, tractable, IBM to predict the ESS for allocation to foliage, wood and fine roots in trees competing for light and nitrogen. Weng et al. (2015) then coupled this game theory approach with an individual-based DVM to investigate ESS for allocation at global scale and accounting for height-structured competition in forest ecosystems. Weng et al. (2017) used this integrative model to investigate the trade-off between carbon- and nitrogen-use efficiency, and the resulting trade-off in functional traits such as leaf mass per unit area and leaf lifetime. Falster et al. (2016) proposed a similar framework, implemented in the R package ‘*plant*’.

**Conclusion** As expected, the number of publications describing physio-demo-genetic models (eight) was even lower than those describing demo-genetic models. The reviewed physio-demo-genetic all explicitly couple a model of trait variation and inheritance with biophysical and demographic models. In this way, they integrate not only the effects of external environmental factors but also endogenous and dynamic factors (e.g. stand structure), on the mortality and reproduction of each individual. Although physio-demo-genetic models are still scarce, their use is expected to increase.

### Scientific challenges

First, a better integration of iVa has been identified as a major priority for ecophysiological models (e.g. Berzaghi et al. 2019; Moran et al. 2016). Indeed, the parameters of ecophysiological PBMs have long been considered as fixed within a species/PFT, while they are likely to vary between environments due to plastic response, and/or among individuals/populations due to heritable genetic or epigenetic differences. Moreover, iVa can have significant effects on simulations with ecophysiological PBMs: an increasing number of studies report that uncertainty on model parameter values is the major cause of uncertainty, sometimes more important than that on climate scenarios (Davi et al. 2006; Jiang et al. 2012; Collalti et al. 2019). Sakschewski et al. (2016) showed that functional trait iVa increases tropical forest resilience to environmental change. The recent review by Berzaghi et al. (2019) distinguishes three ways through which iVa can be incorporated in ecophysiological PBMs. First, these models usually already account for plastic variation, through equations describing a plastic response to a change in biotic and abiotic environment. Secondly, genetic iVa can be incorporated by sampling values of parameters in empirical distributions, considered as prescribed in the model; this strategy may help to understand the role of functional traits iVa in structuring plant communities, although it may fail to predict the role of iVa in the long term. A third strategy is to model explicitly iVa as the result of ecological and evolutionary processes, using the physio-demo-genetic framework. Although computationally costly, such approaches may be necessary, e.g. to evaluate the error made when neglecting the heterogeneity and dynamics of species traits in space and time.

Similarly, there is an increasing interest in incorporating more details on the demographic dynamics and the ecological and environmental context, into evolutionary dynamics models. Donohue et al. (2015) highlight four main interests of PBMs of plant development (e.g. phenological model) to address different processes in evolutionary biology: (i) their ability to link life stages across the life cycle in complex environments; (ii) their ability to incorporate fitness consequences of developmental timing; (iii) thanks to the coupling with population ecology approach, the emerging ability of incorporating population variance to investigate the mechanisms of inter-individual interactions; and (iv) thanks to the incorporation of genetics, the emerging ability to predict genotype-specific reaction norms and environmentaldependent genetic expression. These research perspectives apply more generally to the use of any physiological model in evolutionary biology.

In conclusion, it is clear that integration is long overdue between the physiological responses to the environment, the demographic dynamics and the evolutionary dynamics in PBMs. A methodological advantage for such integration is that evolutionary dynamics, forest dynamics and biophysical PBMs are usually made up of building blocks (submodels) corresponding to major processes. One can thus assemble different pre-existing blocks from various PBMs, particularly when these models are available on common modelling platforms. This approach was used by Kramer et al. (2008) or Oddou-Muratorio and Davi (2014). Although they focused on a specific set of functional traits, their approach can, in theory, be generalized to any functional traits controlled by species-specific parameters in the ecophysiological model. Note that PBMs combining 'only' physiological and genetic processes, without demographic processes, are also of interest in characterizing the genotype-phenotype-fitness map and make a bridge between the demo-genetic and physio-demographic PBMs.

## Data source challenges

Besides the data-related challenges listed above for the other two integrative models, a specific challenge in developing physio-demo-genetic models is to integrate heritable iVa for functional traits in ecophysiological models. The main problem is that the knowledge on plastic versus genetic variation of functional or life-history traits is usually available in different datasets because they are not studied by the same scientific communities. Ecophysiologists' databases may under-evaluate the iVa of functional traits (e.g. when provenance tests are based only on a few number of parents and neglect the family structure in their experimental design) while geneticists' databases usually badly evaluate environmental conditions relevant to the measured traits (for instance, water stress intensity is not measured according to classical physiological standards). However, these issues have been overcome in the case of short-lived species (e.g. Arntz and Delph 2001; Geber and Griffen 2003; Donovan et al. 2011), so we can hope they will be solved in the case of trees (see Maherali et al. 2006). Nested provenance/progeny tests provide an opportunity to measure functional or life-history traits variation and disentangle its components.

## A roadmap for integrating ecophysiological, demographic and/or evolutionary processes

This last section aims to guide ecological modellers to choose the best option for integrating physiological, demographic and/or evolutionary processes in a PBM. Central to this is the precise formulation of the focal issue to address with the model, which should drive the choice of the processes to integrate, as well as the spatial and temporal resolution required for iVa in these processes. Once the processes to integrate have been chosen, some caution should be brought to evaluate model complexity, and to choose the way the model can be lined with data for calibration and validation.

## Which type of integration for which issue?

While demographic-driven, physiological-driven or evolutionary-driven modelling approaches remain pertinent in many cases, some specific issues require the integration of physiological, demographic and/or evolutionary processes (Table 2).

Most importantly, the temporal scale over which the forest dynamics needs to be simulated guides the choice of models and processes to be integrated (Fig. 3). On the short timescale of one tree generation, environmental factors and management are the main drivers of the forest response, while the role of evolutionary drivers of change increases at multi-generational timescale. Physio-demographic models are suitable for issues on short timescales (but possibly large spatial scales), such as investigating the functional consequences of diversity, the demographic impacts of functional traits combinations or the forms of fitness landscapes (e.g. issues 1 or B in Table 2). By contrast, demo-genetic or physio-demo-genetic models are appropriate for issues related to phenotypic change over a few generations, rather at a local scale, for instance to evaluate the plastic and genetic components of phenotypic change (e.g. issues 3 or D in Table 2).

Different types of integration can often be used to address a given issue. Simulated evolutionary rates under GC (e.g. issues 2, E in Table 2) may differ when using a demo-genetic PBM accounting for the heredity and selection of life-history traits (such as growth rate, age at first reproduction), or a physio-demo-genetic PBM accounting for the heredity and selection of functional traits (such as vulnerability to cavitation, water-use efficiency or frost resistance). This is not only because the simulated evolutionary rates obviously consider different traits but also because these approaches rely on different hypotheses. In a physio-demo-genetic approach, evolution is explicitly driven by climate and soil factors through tree physiology, and possible trade-offs between functional traits mediating tree response to climate variation are part of the modelled physiological processes. In a demo-genetic approach, the drivers of environmental change are more abstracted and may be diverse (e.g. they can combine different disturbances such a drought and biotic stresses). Demo-genetic models bypass detailed knowledge of the mechanisms of response, while physio-demo-genetic models incorporate the known physiological mechanisms of response but with higher computational cost.

**Table 2** Examples of key issues on forest adaptive response to GC requiring some coupling between physiological, demographic and/or evolutionary processes. The temporal scale (TS) of the studied response can be within generation (wG) or among-generation (aG). Different levels of spatial resolution of inter-individual variation (iVa) are distinguished (from individual scale to PFTs, see Fig. 3)

| Issues | | TS | Required resolution for iVa |
|---|---|---|---|
| Society-driven issues | | | |
| 1 | How can adaptive management practices, both in terms of choice of forest reproductive material and silviculture, mitigate forest vulnerability to GC on the short-term? | wG | Individual/provenance/species/PFT |
| 2 | How can adaptive silviculture strategies mitigate forest tree populations' vulnerability to GC on the long-term? | aG | Individual |
| 3 | What are the evolutionary costs and benefits of adaptive silviculture strategies to GC at the forestry timescale (~ 200 years)? How can we compromise the short- and long-term costs and benefits of forest management practices? | wG and aG | Individual |
| 4 | How will GC re-arrange the genetic variability in space and time (from forest communities, to intraspecific genetic diversity)? How GC will affect the power of forestry practices? | wG or aG | Individual or population |
| 5 | How can forest management increase the resilience of forest ecosystem services in the context of GC? | wG or aG | From individual to PFT |
| Science-driven issues | | | |
| A | How do plasticity and local adaptation respectively shape the levels of phenotypic diversity and its distribution within and among populations? How may these patterns change under GC? | wG | Individual or population |
| B | How does phenotypic selection change under a changing environment? | wG and aG | Individual |
| C | What processes make the fundamental and realized niches of a species different? | wG | Population |
| D | What is the relative importance of rapid evolutionary change versus plastic change in driving population dynamics? | aG | Individual |
| E | How genetic diversity and evolution can mitigate the vulnerability of a tree population to environmental change and eventually rescue it from extinction? | wG and aG | Individual |

Finally, the need to explicitly simulate the impact of forest management practices on adaptation imposes integrating demographic with either physiological or evolutionary processes. As detailed in Lefèvre et al. (2014), most forestry practices which impact the evolution and evolvability of forest populations consist of demographic control at stand or forest level (e.g. through thinning, regeneration felling and forest planning, including rotation length). Furthermore, each single practice has multiple impacts on the physiological and evolutionary processes and interferes with other practices, and a dynamic approach of these interactions is required. Hence, integrating evolutionary considerations into adaptive forestry practice can enhance the capacity of managed forests to respond to climate-driven changes, and integrative PBMs are appropriate tools to evaluate quantitatively the effects of evolution-oriented forestry practices and to assist forest managers in their implementation.

## Which resolution of phenotypic variation is required?

Different spatial levels of resolution of the phenotypic variation can be considered: among plant functional types (PFT), among species within communities, among provenances within species, or among individuals within populations (Fig. 3). The level of resolution should be appropriately chosen depending on the issue. Another important choice concerns the evolvability of phenotypic variation. For issues related to levels and structure of diversity (e.g. issues 1 or B in Table 2), phenotypic variation does not need to be evolvable and can thus be fixed or randomly generated (e.g. trait values can be drawn in empirical distributions). This is also done in species distribution models (SDM) accounting for local adaptation and phenotypic plasticity in fitness-related traits (Benito-Garzón et al. 2019). With these SDMs, the plastic and genetic component of iVa at key adaptive traits is first

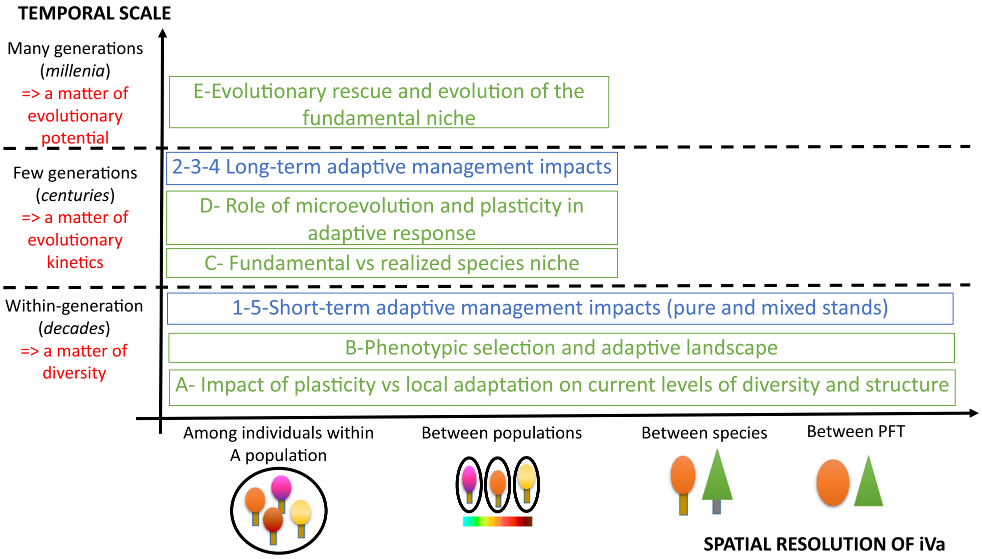


**Fig. 3** The temporal scale and spatial resolution of inter-individual variability (iVa) required to address different issues related to adaptive dynamics of forest under environmental change. Letters and numbers refer to issues listed in Table 2. At the bottom, the focus is on patterns and dynamics of diversity over a short temporal scale (within generation), which can be simulated using physio-demographic models. In the middle, the focus is on non-equilibrium dynamics of diversity over a few generations, which can be simulated using demo-genetic or physio-demo-genetic models. At the top, the focus is on equilibrium dynamics of diversity over many generations, for which demo-genetic models are more appropriate

inferred from multi-site provenance tests, and then, the correlation between phenotype and fitness (inferred from species presence) over large-scale geographic gradients provides a distribution of possible responses under future climates. Eventually, the envelope of iVa can progressively erode while some types locally go extinct, allowing a first level of temporal evolution.

By contrast, any question on a multi-generational timescale requires the iVa to evolve dynamically, driven by the genetic drift and selection processes which dynamically result from the model. Three conditions are required for a model to reach this level: (i) the model must be individual-based; (ii) the model must describe the genetic architecture of the trait variation; and (iii) sexual reproduction processes must be included in the demographic part of the model. For quantitative traits, the 'real' genetic architecture is generally not known in trees; it may even be considered as a kind of illusion since it changes across environments and across populations. However, breeding experience has shown that classical hypotheses in quantitative genetics are robust; hence, based on such hypotheses, there are solutions to simulate individual genotypes that optimally fit the expected genetic parameters at population level for model initialization. Models with evolvable iVa are also more demanding than those with fixed variation.

## How to integrate multiple processes while limiting model's complexity?

This review highlights how physio-demographic, demo-genetic or physio-demo-genetic PBMs allow fitness to emerge from the physiological or demographic response to environmental variation, by considering explicitly interactions between the nested ecological demographic, or/and evolutionary timescales. These emergent properties justify the use of a complex, integrative model, if the question of interest requests it (Table 3). However, critical to the development of integrative models is the achievement of a balance between the 'brute-force approach' (sensu Levins 1966) that attempts to integrate everything in over-complex models, and an over-simplification that discards important biological diversity and environmental heterogeneities at various levels. Levins (1966) explained how describing most of the complexity of interactions between individuals and environment leads to a deadlock. He rather advised the choosing among three strategies and making the 'sacrifice' of one property (between generality, accuracy and realism) to better save the other two. In our opinion, despite the amount of data provided by observational and experimental networking and in spite of computing power having increased, his criticism remains true. In particular, it is hardly possible to have both a 'generic' model applicable to a very broad number of situations and an 'accurate' model able to account for a particular situation.

For each general question and each particular ecological system studied, it is first necessary to build the most cost-effective representation and, therefore, to choose the appropriate modelling tool, the processes to represent and the extent and resolution of the spatial and temporal scales required. As highlighted by Getz et al. (2018), the development of integrative PBM should follow a set of model's adequacy assessment protocols, regarding the selection of state and control

**Table 3** Main features of the integrated demo-genetic, physio-demographic and physio-demo-genetic PBMs reviewed here

| Strengths | Weaknesses |
|---|---|
| Able to simulate non-stationary eco-evolutionary dynamics in a context of change | Require knowledge on multiple processes |
| Account for complexity and contingency of ecological system | High computational complexity |
| Useful both for corroboratory predictions and knowledge building, and for horizon scanning and anticipatory predictions | Complex validation and possible low predictability |
| Opportunities | Threats |
| Increasing number of modelling platforms offering libraries of processes | Difficulty in evaluating the costs and benefits of integrative PBMs as compared to other modelling tools (simpler PBMs, correlative approaches) |
| Increasing amount of data and databases | |
| Increasing computational power | |

variables, the determinacy of data, and the sensitivity and validation of model outputs. Care should be granted to improve the model performances, using refinement or coarse-graining procedures. Finally, an advantage of the integrative PBMs considered in this review is that their results can and should be compared with the simpler ecophysiological, demographic or evolutionary PBMs they derive from, to precisely evaluate the change in model predictions resulting from processes integration. This can be done by simulating baseline scenarios without processes integration (e.g. Oddou-Muratorio and Davi 2014).

From a methodological point of view, it would be best to be able to build custom-made PBMs from libraries of processes described on common modelling platforms, to parameterize these PBMs from empirical databases and to evaluate their outputs using other types of data. PBMs are useful to select the most meaningful adaptive traits to work on (Aubin et al. 2016), through sensitivity analyses and the identification of parameters which have a major effect.

## How can we link integrative PBMs to data?

As illustrated in this review, the availability of experimental data to calibrate and validate PBMs is challenging, particularly for demographic and evolutionary processes. The development of databases is definitely required to tackle these issues. Overall, as compared to databases available for functional or growth traits, databases on quantitative genetic parameters for performance and functional traits lag behind (Table 1). Even though a few reviews provided ranges of values of heritabilities, genetic correlations or other parameters for some traits of interest (Cornelius 1994; Hall et al. 2016; Lind et al. 2018), it is urgent to strengthen the effort to assemble this information in databases available to the community, along the line of H2DB database (an annotation database of genetic heritability estimates for humans and other species; Kaminuma et al. 2013). Moreover, the available empirical data generally refer to past environmental conditions, and the few controlled experiments aiming to test for future conditions in forest systems are restricted to a very limited number of parameters (e.g. FACE experiments: https://facedata.ornl.gov/facemds/). Hence, we probably need new measurements both in natural and controlled conditions meeting all of the standards of the different involved disciplines.

Beyond the data needed to estimate model parameters, a crucial issue is that of the sufficient availability of additional data to carry out robust assessment of the reliability of the integrative PBMs performances. Conceptual and methodological issues related to ecological model validation have been discussed elsewhere in a general way (Rykiel 1996). The higher the number of processes included in any simulation PBM, the more complex the validation is expected to be. The core of this discussion is that the validation of an integrative PBM may require the validation of both each submodel involved in the coupling and also the interfaces between these submodels. Validation based on the comparison of simulated versus observation data may clearly be limited, in particular due the paucity of data on tree response on an evolutionary timescale. However, different types and criteria of validation can be applied, depending on the data and understanding available for the system being modelled (Rykiel 1996). In the case of the integrative PBMs considered here, conceptual validity, defined as the acceptable justification of the scientific content of the model, may be more meaningful and useful than data validity, defined as the demonstration that the model can reproduce observation data. Berzaghi et al. (2019) underlined that data can enter the model at different levels—as inputs, as drivers, as priors on model parameters or as model outputs. In this later case, inverse modelling approaches such as approximate Bayesian computation or other methods are also useful tools to infer model parameters (Piou et al. 2009; Hartig et al. 2011). Solving these calibration and validation issues is crucial to determine the extent to which the integrative PBMs can be considered as models for understanding, or considered as sufficiently reliable to allow forecasting.

In the specific context of the demo-genetic and physio-demo-genetic model considered here, the use of genomic data for calibration of validation may raise (Rudman et al. 2018). As far as trees are concerned, genomic approaches can contribute to the evaluation of target trait heritability in situ. There is also room for demo-genetic and physio-demo-genetic approaches to generate predictions on trait genetic architecture, which may become testable through population genomics approaches. Moreover, because most adaptive traits in trees are highly polygenic (Alberto et al. 2013), the quantitative genetic model provides an efficient framework to represent the genetic architecture of relevant traits for calibrating PBMs.

## Conclusions

The physio-demographic, demo-genetic and physio-demo-genetic PBMs reviewed here rely on the assembly of multiple components interacting with each other. We argue that such models are useful for corroboratory predictions and knowledge building in basic science on the one hand and for anticipatory predictions and horizon scanning of possible future scenarios in applied science on the other hand (Maris et al. 2018). Regarding corroboratory predictions, the main advantage of integrative models is first to explicitly tackle the complexity of ecological systems. Moreover, accounting for iVa in physiological and demographic processes also allows for the addressing of the historical contingency of ecological systems related to their evolutionary history. Integrative PBMs could thus contribute to the removal of these two major obstacles for corroboratory predictions and thereby improve our understanding of ecosystem response to GC.

By shedding light on the interactions between forest functions, forest dynamics and forest genetic diversity, integrative models improve our understanding of the dynamic response to GC. In doing so, they also reveal new complexities, which can be seen as disturbing for anticipatory predictions and decision-making. However, we claim that these models are necessary and useful in the context of GC, when a major issue for forestry is to cope with multiple uncertainties: both short-term and long-term impacts of current decisions must be considered jointly, and adaptive management strategies are emerging (see Yousefpour et al. 2012 for a review). Moreover, as pointed out by Maris et al. (2018), we argue that the need for answers to these pressing environmental problems cannot wait for the corroboratory predictive powers of theory to be improved. Following such strategies, these models should be used in horizon scanning and exploratory scenario approaches (Morán-Ordóñez et al. 2019), rather than attempts at a single future forecast. These models will also be useful in assessing the possible impacts of previous decisions in the adaptive management loop. We have also shown that there are multiple ways to integrate eco-evolutionary processes, and each type of model provides part of the knowledge. It is important that the scientific communities who develop these different ways of eco-evolutionary integration continue their dialogue and do not diverge completely, because accompanying methods to deal with the plurality of predictions are also required.

**Acknowledgments** We are grateful to numerous URFM colleagues (A. Amm, M. Alleaume-Benharira, A. Bontemps, M. Cailleret, C. Pichot, I. Scotti) for the discussions and comments on a previous version of this manuscript.

**Author contributions** FL searched the literature for models integrating demographic and evolutionary processes, HD for models integrating demographic and physiological processes and SOM for models integrating physiological, demographic and evolutionary processes. All the authors drafted the manuscript and SOM coordinated the assembly.

**Funding information** This study was partly funded by the European Union's Horizon 2020 research and innovation programme, under Grant Agreement No. 676876 (GenTree) and No. 773383 (B4EST).

## Glossary

**Adaptive or evolutionary dynamics** : the regime of change in the genetic composition of a population across generations.

**Demographic (or vital) rates** : refer to how fast demographic statistics (e.g. the number of death and births) change in a population. At population level, they are usually expressed as number (of deaths, or birth) scaled by population size and expressed per unit of time. They can also be expressed at cohort or individual level, as individual probabilities per unit of time (e.g. age-specific survival probability or expected fecundity). Demographic rates are the outcomes of the interaction between traits (e.g. size) and environment.

**Fitness** : the number of offspring produced by a given phenotype or genotype over its lifetime that reach maturity.

**Genetic adaptation** : genetic response of a population to selection through changes in DNA sequence between generations, resulting in phenotypic change and increasing fitness.

**Life-history trait** : an individual characteristic contributing to life-history strategy (i.e. a change in that trait creates the most significant difference in fitness). Major life-history traits are size at birth, growth rate, age and size at maturity, number and size of offspring, age- and size-specific reproductive investments.

**Functional trait** : any observable characteristic of an individual, including morphological, physiological or phenological characteristics, which influences the demographic and reproductive performances or ecological functions of this plant.

**Performance** : an individual characteristic recognized as good proxy of the survival or reproductive components of fitness. In trees, growth is often used as a predictor of survival, while characteristics such as seed output and seed mass are usually considered as good proxies of fecundity. Population ecologists often consider these plant performances as demographic/vital rates, while evolutionary ecologists consider them as life-history traits.

**Phenotypic plasticity**: the phenomenon of the same genotype producing different phenotypes in response to different environmental stimuli.

**Population dynamics** : the regime of change in demographic composition (size, age structure) through time.

**Process-based (or mechanistic) model**: models that characterize the dynamics of a system (through the description of its internal mechanisms) as explicit functions of component parts and their associated actions and interactions.

**Resistance**: capacity of a population or an individual to remain stable and limit the negative impact of an external pressure.

**Resilience**: in a strict sense, it is the capacity of a population or an individual to persist to an external pressure despite response changes (persistent unstable system); in a broad sense, it also includes resistance.

**The genotype-phenotype-fitness map**: is a composite framework proposed by Coulson et al. (2006) that maps different levels of biological diversity onto one another. Each individual map is environment-dependent, and the integrative PBMs integrate the fact that part of the environment dynamically evolves with the demographic structure (Fig. 2). It includes three components:

- **The genotype-phenotype map**: specifies the link between alleles, the proteins they code for and phenotypic traits. The genotype-phenotype map potentially includes epistatic interactions among several genes on a single trait or pleiotropic effect of a single gene on several traits (pleiotropy can result dynamically from the model).
- **The phenotype-demography map** : describes the changes in the values of demographic rates resulting from changes in the values of the traits. Its aim is to identify the association between the value of a phenotypic trait and the probability of an individual expressing that trait value surviving, reproducing or dispersing. It accounts for phenotype-by-environment interactions. The associations between *all* traits and *all* demographic rates ultimately describes population growth (the mean demography). The phenotype-demography map may include functional effects comparable to genetic epistasis (interaction effects of several traits on a single demographic rate) or pleiotropy (multiple effects of a single trait on several demographic rates).
- **The demography-fitness map** : describes the way that trait variation contributes to individual variation in fitness via demography and hence provides opportunity for selection. The original formulation by Coulson et al. (2006) relates to mean fitness, i.e. population growth rate in the matrix populations models' framework.

## References

Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD, Anderegg LDL, Barron-Gafford GA, Beerling DJ, Breshears DD, Brodribb TJ, Bugmann H, Cobb RC, Collins AD, Dickman LT, Duan H, Ewers BE, Galiano L, Galvez DA, Garcia-Forner N, Gaylord ML, Germino MJ, Gessler A, Hacke UG, Hakamada R, Hector A, Jenkins MW, Kane JM, Kolb TE, Law DJ, Lewis JD, Limousin JM, Love DM, Macalady AK, Martínez-Vilalta J, Mencuccini M, Mitchell PJ, Muss JD, O'Brien MJ, O'Grady AP, Pangle RE, Pinkard EA, Piper FI, Plaut JA, Pockman WT, Quirk J, Reinhardt K, Ripullone F, Ryan MG, Sala A, Sevanto S, Sperry JS, Vargas R, Vennetier M, Way DA, Xu C, Yepez EA, McDowell NG (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nature Ecol Evol 1:1285–1291. https://doi.org/10.1038/s41559-017-0248-x

Alberto FJ, Aitken SN, Alía R et al (2013) Potential for evolutionary responses to climate change—evidence from tree populations. Glob Chang Biol 19:1645–1661. https://doi.org/10.1111/gcb.12181

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH(T), Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Anderegg WRL, Kane JM, Anderegg LDL (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. Nat Clim Chang 3:30–36. https://doi.org/10.1038/nclimate1635

Arntz MA, Delph LF (2001) Pattern and process: evidence for the evolution of photosynthetic traits in natural populations. Oecologia 127:455–467. https://doi.org/10.1007/s004420100650

Atkin OK, Bloomfield KJ, Reich PB, Tjoelker MG, Asner GP, Bonal D, Bönisch G, Bradford MG, Cernusak LA, Cosio EG, Creek D, Crous KY, Domingues TF, Dukes JS, Egerton JJG, Evans JR, Farquhar GD, Fyllas NM, Gauthier PPG, Gloor E, Gimeno TE, Griffin KL, Guerrieri R, Heskel MA, Huntingford C, Ishida FY, Kattge J, Lambers H, Liddell MJ, Lloyd J, Lusk CH, Martin RE, Maksimov AP, Maximov TC, Malhi Y, Medlyn BE, Meir P, Mercado LM, Mirotchnick N, Ng D, Niinemets Ü, O'Sullivan OS, Phillips OL, Poorter L, Poot P, Prentice IC, Salinas N, Rowland LM, Ryan MG, Sitch S, Slot M, Smith NG, Turnbull MH, VanderWel MC, Valladares F, Veneklaas EJ, Weerasinghe LK, Wirth C, Wright IJ, Wythers KR, Xiang J, Xiang S, Zaragoza-Castells J (2015) Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. New Phytol 206:614–636. https://doi.org/10.1111/nph.13253

Aubin I, Munson A, Cardou F et al (2016) Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. Environ Rev 24:164–186. https://doi.org/10.1139/er-2015-0072

Austerlitz F, Garnier-Géré PH (2003) Modelling the impact of colonisation on genetic diversity and differentiation of forest trees: interaction of life cycle, pollen flow and seed long-distance dispersal. Heredity 90:282–290. https://doi.org/10.1038/sj.hdy.6800243

Austerlitz F, Mariette S, Machon N, Gouyon PH, Godelle B (2000) Effects of colonization processes on genetic diversity: differences between annual plants and tree species. Genetics 154:1309–1321

Babst F, Poulter B, Trouet V et al (2013) Site- and species-specific responses of forest growth to climate across the European continent. Glob Ecol Biogeogr 22:706–717. https://doi.org/10.1111/geb.12023

Bellassen V, Le Maire G, Dhote JF et al (2010) Modelling forest management within a global vegetation model part 1: model structure and general behaviour. Ecol Model 221:2458–2474. https://doi.org/10.1016/j.ecolmodel.2010.07.008

Benito-Garzón M, Robson TM, Hampe A (2019) ΔTraitSDMs: species distribution models that account for local adaptation and phenotypic plasticity. New Phytol 222:1757–1765. https://doi.org/10.1111/nph.15716

Berzaghi F, Bohn F, Kramer K et al (2019) Towards a new generation of trait-flexible vegetation models. Trends Ecol Evol 35:191–205. https://doi.org/10.1016/j.tree.2019.11.006

Bontemps A, Davi H, Lefèvre F et al (2017) How do functional traits syndromes covary with growth and reproductive performance in a water-stressed population of Fagus sylvatica? Oikos 126:1472–1483. https://doi.org/10.1111/oik.04156

Bost B, De Vienne D, Hospital F et al (2001) Genetic and nongenetic bases for the L-shaped distribution of quantitative trait loci effects. Genetics 157:1773–1787 https://www.genetics.org/content/157/4/1773

Boulangeat I, Georges D, Dentant C, Bonet R, van Es J, Abdulhak S, Zimmermann NE, Thuiller W (2014) Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. Ecography 37:1230–1239. https://doi.org/10.1111/ecog.00694

Briceno-Elizondo E, Garcia-Gonzalo J, Peltola H et al (2006) Sensitivity of growth of scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. For Ecol Manag 232:152–167. https://doi.org/10.1016/j.foreco.2006.05.062

Broadhurst LM, Young AG, Forrester R (2008) Genetic and demographic responses of fragmented Acacia dealbata (Mimosaceae) populations in southeastern Australia. Biol Conserv 141:2843–2856. https://doi.org/10.1016/j.biocon.2008.08.021

Buckley TN, Roberts DW (2006) DESPOT, a process-based tree growth model that allocates carbon to maximize carbon gain. Tree Physiol 26:129–144. https://doi.org/10.1093/treephys/26.2.129

Bugmann H (1996) A simplified forest model to study species composition along climate gradients. Ecology 77:2055–2074. https://doi.org/10.2307/2265700

Bugmann H (2001) A review of forest gap models. Clim Chang 196:259–305. https://doi.org/10.1023/A:1012525626267

Case M, Lawler J (2017) Integrating mechanistic and empirical model projections to assess climate impacts on tree species distributions in northwestern North America. Glob Chang Biol 23:2005–2015. https://doi.org/10.1111/gcb.13570

Chauvet M, Kunstler G, Roy J, Morin X (2017) Using a forest dynamics model to link community assembly processes and traits structure. Funct Ecol 31:1452–1461. https://doi.org/10.1111/1365-2435.12847

Chave J, Norden N (2007) Changes of species diversity in a simulated fragmented neutral landscape. Ecol Model 207:3–10. https://doi.org/10.1016/j.ecolmodel.2007.03.025

Cheaib A, Badeau V, Boe J, Chuine I, Delire C, Dufrêne E, François C, Gritti ES, Legay M, Pagé C, Thuiller W, Viovy N, Leadley P (2012) Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. Ecol Lett 15:533–544. https://doi.org/10.1111/j.1461-0248.2012.01764.x

Chuine I, Beaubien EG (2001) Phenology is a major determinant of tree species range. Ecol Lett 4:500–510. https://doi.org/10.1046/j.1461-0248.2001.00261.x

Collalti A, Thornton PE, Cescatti A, Rita A, Borghetti M, Nolè A, Trotta C, Ciais P, Matteucci G (2019) The sensitivity of the forest carbon budget shifts across processes along with stand development and climate change. Ecol Appl 29:e01837. https://doi.org/10.1002/eap.1837

Coltman DW (2005) Testing marker-based estimates of heritability in the wild. Mol Ecol 14:2593–2599. https://doi.org/10.1111/j.1365-294X.2005.02600.x

Cornelius J (1994) Heritabilities and additive genetic coefficients of variation in forest trees. Can J For Res 24:372–379. https://doi.org/10.1139/x94-050

Coulson T, Benton TG, Lundberg P et al (2006) Putting evolutionary biology back in the ecological theatre: a demographic framework mapping genes to communities. Evol Ecol Res 8:1155–1171

Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models. Glob Chang Biol 7:357–373. https://doi.org/10.1046/j.1365-2486.2001.00383.x

Davi H, Cailleret M (2017) Assessing drought-driven mortality trees with physiological process-based models. Agric For Meteorol 232:279–290. https://doi.org/10.1016/j.agrformet.2016.08.019

Davi H, Dufrêne E, Francois C, le Maire G, Loustau D, Bosc A, Rambal S, Granier A, Moors E (2006) Sensitivity of water and carbon fluxes to climate changes from 1960 to 2100 in European forest ecosystems. Agric For Meteorol 141:35–56. https://doi.org/10.1016/j.agrformet.2006.09.003

de Lacerda AEB, Roberta Nimmo E, Sebbenn AM (2013) Modeling the long-term impacts of logging on genetic diversity and demography of Hymenaea courbaril. For Sci 59:15–26. https://doi.org/10.5849/forsci.10-118

Degen B, Roubik DW (2004) Effects of animal pollination on pollen dispersal, selfing, and effective population size of tropical trees: a simulation study 1. Biotropica 36:165. https://doi.org/10.1646/q1554

Degen B, Gregorius HR, Scholz F (1996) ECO-GENE, a model for simulation studies on the spatial and temporal dynamics of genetic structures of tree populations. Silvae Genetica 45:323–329

Degen B, Blanc L, Caron H et al (2006) Impact of selective logging on genetic composition and demographic structure of four tropical tree species. Biol Conserv 131:386–401. https://doi.org/10.1016/j.biocon.2006.02.014

Difazio SP, Leonardi S, Slavov GT et al (2012) Gene flow and simulation of transgene dispersal from hybrid poplar plantations. New Phytol 193:903–915. https://doi.org/10.1111/j.1469-8137.2011.04012.x

Ditzer T, Glauner R, Forster M, Kohler P, Huth A (2000) The process-based stand growth model Formix 3-Q applied in a GIS environment for growth and yield analysis in a tropical rain forest. Tree Physiol 20:367–381

Donohue K, Burghardt LT, Runcie D, Bradford KJ, Schmitt J (2015) Applying developmental threshold models to evolutionary ecology. Trends Ecol Evol 30:66–77. https://doi.org/10.1016/j.tree.2014.11.008

Donovan LA, Maherali H, Caruso CM, Huber H, de Kroon H (2011) The evolution of the worldwide leaf economics spectrum. Trends Ecol Evol 26:88–95. https://doi.org/10.1016/j.tree.2010.11.011

Dufrêne E, Davi H, François C et al (2005) Modelling carbon and water cycles in a beech forest. Ecol Model 185:407–436. https://doi.org/10.1016/j.ecolmodel.2005.01.004

Dunlop ES, Heino M, Dieckmann U (2009) Eco-genetic modeling of contemporary life-history evolution. Ecol Appl 19:1815–1834. https://doi.org/10.1890/08-1404.1

Dybzinski R, Farrior C, Wolf A, Reich PB, Pacala SW (2011) Evolutionarily stable strategy carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. Am Nat 177:153–166. https://doi.org/10.1086/657992

Evans MR (2012) Modelling ecological systems in a changing world. Philos Trans R Soc B 367:181–190. https://doi.org/10.1098/rstb.2011.0172

Evans MR, Grimm V, Johst K et al (2013) Do simple models lead to generality in ecology? Trends Ecol Evol 28:578–583. https://doi.org/10.1016/j.tree.2013.05.022

Falster DS, Fitzjohn RG, Brännström AA et al (2016) Plant: a package for modelling forest trait ecology and evolution. Methods Ecol Evol 7:136–146. https://doi.org/10.1111/2041-210X.12525

Fang J, Lutz JA, Shugart HH, Yan X (2019) A physiological model for predicting dynamics of tree stem-wood non-structural carbohydrates. J Ecol 0:1–17. https://doi.org/10.1111/1365-2745.13274

Favrichon V (1997) Apports d ' un modèle démographique plurispécifique pour l 'étude des relations diversité/dynamique en forêt tropicale guyanaise. Ann Sci For 55:655–669

Fischer R, Bohn F, Dantas de Paula M et al (2016) Lessons learned from applying a forest gap model to understand ecosystem and carbon dynamics of complex tropical forests. Ecol Model 326:124–133. https://doi.org/10.1016/j.ecolmodel.2015.11.018

Fisher R, McDowell N, Purves D et al (2010) Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. New Phytol 187:666–681. https://doi.org/10.1111/j.1469-8137.2010.03340.x

Fujii S, Kubota Y, Enoki T (2009) Resilience of stand structure and tree species diversity in subtropical forest degraded by clear logging. J For Res 14:373–387. https://doi.org/10.1007/s10310-009-0151-7

Gea-Izquierdo G, Nicault A, Battipaglia G et al (2017) Risky future for Mediterranean forests unless they undergo extreme carbon fertilization. Glob Chang Biol 23:2915–2927. https://doi.org/10.1111/gcb.13597

Geber MA, Griffen LR (2003) Inheritance and natural selection on functional traits. Int J Plant Sci 164:S21–S42. https://doi.org/10.1086/368233

Getz WM, Marshall CR, Carlson CJ, Giuggioli L, Ryan SJ, Romañach SS, Boettiger C, Chamberlain SD, Larsen L, D'Odorico P, O'Sullivan D (2018) Making ecological models adequate. Ecol Lett 21:153–166. https://doi.org/10.1111/ele.12893

Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke HH, Weiner J, Wiegand T, DeAngelis D (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991. https://doi.org/10.1126/science.1116681

Guillemot J, Martin-StPaul NK, Dufrêne E et al (2015) The dynamic of annual carbon allocation to wood in European forests is consistent with a combined source-sink limitation of growth: implications for modelling. Biogeosci Discuss 12:2213–2255. https://doi.org/10.5194/bgd-12-2213-2015

Gutierrez AG, Snell RS, Bugmann H (2016) Using a dynamic forest model to predict tree species distributions. Glob Ecol Biogeogr 25:347–358. https://doi.org/10.1111/geb.12421

Hall D, Hallingbäck HR, Wu HX, Hall D (2016) Estimation of number and size of QTL effects in forest tree traits. Tree Genet Genomes 12:1–17. https://doi.org/10.1007/s11295-016-1073-0

Halofsky JS, Conklin DR, Donato DC et al (2018) Climate change, wildfire, and vegetation shifts in a high-inertia forest landscape: Western Washington, U.S.A. PLoS One 13:1–23. https://doi.org/10.1371/journal.pone.0209490

Hanski I (2012) Eco-evolutionary dynamics in a changing world. Ann N Y Acad Sci 1249:1–17. https://doi.org/10.1111/j.1749-6632.2011.06419.x

Hartig F, Calabrese JM, Reineking B et al (2011) Statistical inference for stochastic simulation models—theory and application. Ecol Lett 14:816–827. https://doi.org/10.1111/j.1461-0248.2011.01640.x

Hendry AP (2016) Eco-evolutionary dynamics. Princeton University Press

Henry M, Bombelli A, Trotta C, et al. (2013) GlobAllomeTree: international platform for tree allometric equations to support volume, biomass and carbon assessment. iForest - biogeosciences and forestry 6:326. https://doi.org/10.3832/ifor0901-006

Hoebee SE, Thrall PH, Young AG (2008) Integrating population demography, genetics and self-incompatibility in a viability assessment of the wee Jasper Grevillea (*Grevillea iaspicula* McGill., Proteaceae). Conserv Genet 9:515–529. https://doi.org/10.1007/s10592-007-9366-3

Hulsmann L, Bugmann H, Cailleret M, Brang P (2018) How to kill a tree: empirical mortality models for 18 species and their performance in a dynamic forest model. Ecol Appl 28:522–540. https://doi.org/10.1002/eap.1668

Jansen M, Zuidema PA, Anten NPR, Martínez-Ramos M (2012) Strong persistent growth differences govern individual performance and population dynamics in a tropical forest understorey palm. J Ecol 100:1224–1232. https://doi.org/10.1111/j.1365-2745.2012.02001.x

Jeltsch F, Moloney KA, Schurr FM, Köchy M, Schwager M (2008) The state of plant population modelling in light of environmental change. Perspec Plant Ecol Evol Syst 9:171–189. https://doi.org/10.1016/j.ppees.2007.11.004

Jiang Y, Zhuang Q, Schaphoff S, Sitch S, Sokolov A, Kicklighter D, Melillo J (2012) Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. Ecol Evol 2:593–614. https://doi.org/10.1002/ece3.85

Jolivet C, Degen B (2011) Spatial genetic structure in wild cherry (Prunus avium L.): II. Effect of density and clonal propagation on spatial genetic structure based on simulation studies. Tree Genet Genomes 7:541–552. https://doi.org/10.1007/s11295-010-0354-2

Kaminuma E, Fujisawa T, Tanizawa Y, Sakamoto N, Kurata N, Shimizu T, Nakamura Y (2013) H2DB: a heritability database across multiple species by annotating trait-associated genomic loci. Nucleic Acids Res 41:D880–D884. https://doi.org/10.1093/nar/gks1216

Kammesheidt L, Kohler P, Huth A (2002) Simulating logging scenarios in secondary forest embedded in a fragmented neotropical landscape. For Ecol Manag 170:89–105. https://doi.org/10.1016/S0378-1127(01)00783-6

Kashimshetty Y, Pelikan S, Rogstad SH (2015) Variable gene dispersal conditions and spatial deforestation patterns can interact to affect tropical tree conservation outcomes. PLoS One 10:1–22. https://doi.org/10.1371/journal.pone.0127745

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M, Acosta ATR, Adamidis GC, Adamson K, Aiba M, Albert CH, Alcántara JM, Alcázar C C, Aleixo I, Ali H, Amiaud B, Ammer C, Amoroso MM, Anand M, Anderson C, Anten N, Antos J, Apgaua DMG, Ashman TL, Asmara DH, Asner GP, Aspinwall M, Atkin O, Aubin I, Baastrup-Spohr L, Bahalkeh K, Bahn M, Baker T, Baker WJ, Bakker JP, Baldocchi D, Baltzer J, Banerjee A, Baranger A, Barlow J, Barneche DR, Baruch Z, Bastianelli D, Battles J, Bauerle W, Bauters M, Bazzato E, Beckmann M, Beeckman H, Beierkuhnlein C, Bekker R, Belfry G, Belluau M, Beloiu M, Benavides R, Benomar L, Berdugo-Lattke ML, Berenguer E, Bergamin R, Bergmann J, Bergmann Carlucci M, Berner L, Bernhardt-Römermann M, Bigler C, Bjorkman AD, Blackman C, Blanco C, Blonder B, Blumenthal D, Bocanegra-González KT, Boeckx P, Bohlman S, Böhning-Gaese K, Boisvert-Marsh L, Bond W, Bond-Lamberty B, Boom A, Boonman CCF, Bordin K, Boughton EH, Boukili V, Bowman DMJS, Bravo S, Brendel MR, Broadley MR, Brown KA, Bruelheide H, Brumnich F, Bruun HH, Bruy D, Buchanan SW, Bucher SF, Buchmann N, Buitenwerf R, Bunker DE, Bürger J, Burrascano S, Burslem DFRP, Butterfield BJ, Byun C, Marques M, Scalon MC, Caccianiga M, Cadotte M, Cailleret M, Camac J, Camarero JJ, Campany C, Campetella G, Campos JA, Cano-Arboleda L, Canullo R, Carbognani M, Carvalho F, Casanoves F, Castagneyrol B, Catford JA, Cavender-Bares J, Cerabolini BEL, Cervellini M, Chacón-Madrigal E, Chapin K, Chapin FS, Chelli S, Chen SC, Chen A, Cherubini P, Chianucci F, Choat B, Chung KS, Chytrý M, Ciccarelli D, Coll L, Collins CG, Conti L, Coomes D, Cornelissen JHC, Cornwell WK, Corona P, Coyea M, Craine J, Craven D, Cromsigt JPGM, Csecserits A, Cufar K, Cuntz M, Silva AC, Dahlin KM, Dainese M, Dalke I, Dalle Fratte M, Dang-le AT, Danihelka J, Dannoura M, Dawson S, Beer AJ, de Frutos A, de Long JR, Dechant B, Delagrange S, Delpierre N, Derroire G, Dias AS, Diaz-Toribio MH, Dimitrakopoulos PG, Dobrowolski M, Doktor D, Dřevojan P, Dong N, Dransfield J, Dressler S, Duarte L, Ducouret E, Dullinger S, Durka W, Duursma R, Dymova O, E-Vojtkó A, Eckstein RL, Ejtehadi H, Elser J, Emilio T, Engemann K, Erfanian MB, Erfmeier A, Esquivel-Muelbert A, Esser G, Estiarte M, Domingues TF, Fagan WF, Fagúndez J, Falster DS, Fan Y, Fang J, Farris E, Fazlioglu F, Feng Y, Fernandez-Mendez F, Ferrara C, Ferreira J, Fidelis A, Finegan B, Firn J, Flowers TJ, Flynn DFB, Fontana V, Forey E, Forgiarini C, François L, Frangipani M, Frank D, Frenette-Dussault C, Freschet GT, Fry EL, Fyllas NM, Mazzochini GG, Gachet S, Gallagher R, Ganade G, Ganga F, García-Palacios P, Gargaglione V, Garnier E, Garrido JL, Gasper AL, Gea-Izquierdo G, Gibson D, Gillison AN, Giroldo A, Glasenhardt MC, Gleason S, Gliesch M, Goldberg E, Göldel B, Gonzalez-Akre E, Gonzalez-Andujar JL, González-Melo A, González-Robles A, Graae BJ, Granda E, Graves S, Green WA, Gregor T, Gross N, Guerin GR, Günther A, Gutiérrez AG, Haddock L, Haines A, Hall J, Hambuckers A, Han W, Harrison SP, Hattingh W, Hawes JE, He T, He P, Heberling JM, Helm A, Hempel S, Hentschel J, Hérault B, Hereş AM, Herz K, Heuertz M, Hickler T, Hietz P, Higuchi P, Hipp AL, Hirons A, Hock M, Hogan JA, Holl K, Honnay O, Hornstein D, Hou E, Hough-Snee N, Hovstad KA, Ichie T, Igić B, Illa E, Isaac M, Ishihara M, Ivanov L, Ivanova L, Iversen CM, Izquierdo J, Jackson RB, Jackson B, Jactel H, Jagodzinski AM, Jandt U, Jansen S, Jenkins T, Jentsch A, Jespersen JRP, Jiang GF, Johansen JL, Johnson D, Jokela EJ, Joly CA, Jordan GJ, Joseph GS, Junaedi D, Junker RR, Justes E, Kabzems R, Kane J, Kaplan Z, Kattenborn T, Kavelenova L, Kearsley E, Kempel A, Kenzo T, Kerkhoff A, Khalil MI, Kinlock NL, Kissling WD, Kitajima K, Kitzberger T, Kjøller R, Klein T, Kleyer M, Klimešová J, Klipel J, Kloeppel B, Klotz S, Knops JMH, Kohyama T, Koike F, Kollmann J, Komac B, Komatsu K, König C, Kraft NJB, Kramer K, Kreft H, Kühn I, Kumarathunge D, Kuppler J, Kurokawa H, Kurosawa Y, Kuyah S, Laclau JP, Lafleur B, Lallai E, Lamb E, Lamprecht A, Larkin DJ, Laughlin D, le Bagousse-Pinguet Y, Maire G, Roux PC, Roux E, Lee T, Lens F, Lewis SL, Lhotsky B, Li Y, Li X, Lichstein JW, Liebergesell M, Lim JY, Lin YS, Linares JC, Liu C, Liu D, Liu U, Livingstone S, Llusià J, Lohbeck M, López-García Á, Lopez-Gonzalez G, Lososová Z, Louault F, Lukács BA, Lukeš P, Luo Y, Lussu M, Ma S, Maciel Rabelo Pereira C, Mack M, Maire V, Mäkelä A, Mäkinen H, Malhado ACM, Mallik A, Manning P, Manzoni S, Marchetti Z, Marchino L, Marcilio-Silva V, Marcon E, Marignani M, Markesteijn L, Martin A, Martínez-Garza C, Martínez-Vilalta J, Mašková T, Mason K, Mason N, Massad TJ, Masse J, Mayrose I, McCarthy J, McCormack ML, McCulloh K, McFadden IR, McGill BJ, McPartland MY, Medeiros JS, Medlyn B, Meerts P, Mehrabi Z, Meir P, Melo FPL, Mencuccini M, Meredieu C, Messier J, Mészáros I, Metsaranta J, Michaletz ST, Michelaki C, Migalina S, Milla R, Miller JED, Minden V, Ming R, Mokany K, Moles AT, Molnár A V, Molofsky J, Molz M, Montgomery RA, Monty A, Moravcová L, Moreno-Martínez A, Moretti M, Mori AS, Mori S, Morris D, Morrison J, Mucina L, Mueller S, Muir CD, Müller SC, Munoz F, Myers-Smith IH, Myster RW, Nagano M, Naidu S, Narayanan A, Natesan B, Negoita L, Nelson AS, Neuschulz EL, Ni J, Niedrist G, Nieto J, Niinemets Ü, Nolan R, Nottebrock H, Nouvellon Y, Novakovskiy A, The Nutrient Network, Nystuen KO, O'Grady A, O'Hara K, O'Reilly-Nugent A, Oakley S, Oberhuber W, Ohtsuka T, Oliveira R, Öllerer K, Olson ME, Onipchenko V, Onoda Y, Onstein RE, Ordonez JC, Osada N, Ostonen I, Ottaviani G, Otto S, Overbeck GE, Ozinga WA, Pahl AT, Paine CET, Pakeman RJ, Papageorgiou AC, Parfionova E, Pärtel M, Patacca M, Paula S, Paule J, Pauli H, Pausas JG, Peco B, Penuelas J, Perea A, Peri PL, Petisco-Souza AC, Petraglia A, Petritan AM, Phillips OL, Pierce S, Pillar VD, Pisek J, Pomogaybin A, Poorter H, Portsmuth A, Poschlod P, Potvin C, Pounds D, Powell AS, Power SA, Prinzing A, Puglielli G, Pyšek P, Raevel V, Rammig A, Ransijn J, Ray CA, Reich PB, Reichstein M, Reid DEB, Réjou-Méchain M, Dios VR, Ribeiro S, Richardson S, Riibak K, Rillig MC, Riviera F, Robert EMR, Roberts S, Robroek B, Roddy A, Rodrigues AV, Rogers A, Rollinson E, Rolo V, Römermann C, Ronzhina D, Roscher C, Rosell JA, Rosenfield MF, Rossi C, Roy DB, Royer-Tardif S, Rüger N, Ruiz-Peinado R, Rumpf SB, Rusch GM, Ryo M, Sack L, Saldaña A, Salgado-Negret B, Salguero-Gomez R, Santa-Regina I, Santacruz-García AC, Santos J, Sardans J, Schamp B, Scherer-Lorenzen M, Schleuning M, Schmid B, Schmidt M, Schmitt S, Schneider JV, Schowanek SD, Schrader J, Schrodt F, Schuldt B, Schurr F, Selaya Garvizu G, Semchenko M, Seymour C, Sfair JC, Sharpe JM, Sheppard CS, Sheremetiev S, Shiodera S, Shipley B, Shovon TA, Siebenkäs A, Sierra C, Silva V, Silva M, Sitzia T, Sjöman H, Slot M, Smith NG, Sodhi D, Soltis P, Soltis D, Somers B, Sonnier G, Sørensen MV, Sosinski EE Jr, Soudzilovskaia NA, Souza AF, Spasojevic M, Sperandii MG, Stan AB, Stegen J, Steinbauer K, Stephan JG, Sterck F, Stojanovic DB, Strydom T, Suarez ML, Svenning JC, Svitková I, Svitok M, Svoboda M, Swaine E, Swenson N, Tabarelli M, Takagi K, Tappeiner U, Tarifa R, Tauugourdeau S, Tavsanoglu C, Beest M, Tedersoo L, Thiffault N, Thom D, Thomas E, Thompson K, Thornton PE, Thuiller W, Tichý L, Tissue D, Tjoelker MG, Tng DYP, Tobias J, Török P, Tarin T, Torres-Ruiz JM, Tóthmérész B, Treurnicht M, Trivellone V, Trolliet F, Trotsiuk V, Tsakalos JL, Tsiripidis I, Tysklind N, Umehara T, Usoltsev V, Vadeboncoeur M, Vaezi J, Valladares F, Vamosi J, Bodegom PM, Breugel M, van Cleemput E, Weg M, Merwe S, Plas F, Sande MT, Kleunen M, van Meerbeek K, Vanderwel M, Vanselow KA, Vårhammar A, Varone L, Vasquez Valderrama MY, Vassilev K, Vellend M, Veneklaas EJ, Verbeeck H, Verheyen K, Vibrans A, Vieira I, Villacís J, Violle C, Vivek P, Wagner K, Waldram M, Waldron A, Walker AP, Waller M, Walther G, Wang H, Wang F, Wang W, Watkins H, Watkins J, Weber U, Weedon JT, Wei L, Weigelt P, Weiher E, Wells AW, Wellstein C, Wenk E, Westoby M, Westwood A, White PJ, Whitten M, Williams M, Winkler DE, Winter K, Womack C, Wright IJ, Wright SJ, Wright J, Pinho BX, Ximenes F, Yamada T, Yamaji K, Yanai R, Yankov N, Yguel B, Zanini KJ, Zanne AE, Zelený D, Zhao YP, Zheng J, Zheng J, Ziemińska K, Zirbel CR, Zizka G, Zo-Bi IC, Zotz G, Wirth C (2020) TRY plant trait database – enhanced coverage and open access. Glob Chang Biol 26:119–188. https://doi.org/10.1111/gcb.14904

Kohyama T (1994) Size-structure-based models of forest dynamics to interpret population- and community-level mechanisms. J Plant Res 107:107–116. https://doi.org/10.1007/BF02344537

Kohyama T (2006) The effect of patch demography on the community structure of forest trees. Ecol Res 21:346–355. https://doi.org/10.1007/s11284-006-0168-8

Kramer K, van der Werf B (2010) Equilibrium and non-equilibrium concepts in forest genetic modelling: population- and individually-based approaches. Forest Sys 19:100–112. https://doi.org/10.5424/fs/201019S-9312

Kramer K, Buiteveld J, Forstreuter M, Geburek T, Leonardi S, Menozzi P, Povillon F, Schelhaas MJ, Teissier du Cros E, Vendramin GG, van der Werf DC (2008) Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. Ecol Model 216:333–353. https://doi.org/10.1016/j.ecolmodel.2008.05.004

Kramer K, van der Werf B, Schelhaas M-J (2015) Bring in the genes: genetic-ecophysiological modeling of the adaptive response of trees to environmental change. With application to the annual cycle. Front Plant Sci 5. https://doi.org/10.3389/fpls.2014.00742

Kuparinen A, Schurr FM (2007) A flexible modelling framework linking the spatio-temporal dynamics of plant genotypes and populations: application to gene flow from transgenic forests. Ecol Model 202: 476–486. https://doi.org/10.1016/j.ecolmodel.2006.11.015

Kuparinen A, Savolainen O, Schurr FM (2010) Increased mortality can promote evolutionary adaptation of forest trees to climate change. For Ecol Manag 259:1003–1008. https://doi.org/10.1016/j.foreco.2009.12.006

Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For Ecol Manag 95:209–228. https://doi.org/10.1016/S0378-1127(97)00026-1

Lasky JR, Uriarte M, Boukili VK, Chazdon RL (2014) Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. Proc Natl Acad Sci U S A 111:5616–5621. https://doi.org/10.1073/pnas.1319342111

Le Corre V, Kremer A (2012) The genetic differentiation at quantitative trait loci under local adaptation. Mol Ecol 21:1548–1566. https://doi.org/10.1111/j.1365-294X.2012.05479.x

Le Corre V, Machon N, Petit RJ, Kremer A (1997) Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: a simulation study. Genet Res 69: 117–125. https://doi.org/10.1017/S0016672397002668

Lefèvre F, Boivin T, Bontemps A, Courbet F, Davi H, Durand-Gillmann M, Fady B, Gauzere J, Gidoin C, Karam MJ, Lalagüe H, Oddou-Muratorio S, Pichot C (2014) Considering evolutionary processes in adaptive forestry. Ann For Sci 71:723–739. https://doi.org/10.1007/s13595-013-0272-1

Levins R (1966) The strategy of model building in population biology. Am Sci 54:421–431

Lind BM, Menon M, Bolte CE, Faske TM, Eckert AJ (2018) The genomics of local adaptation in trees: are we out of the woods yet? Tree Genet Genomes 14:29. https://doi.org/10.1007/s11295-017-1224-y

Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ (2006) TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. Ecol Model 199:409–420. https://doi.org/10.1016/j.ecolmodel.2005.11.046

Maherali H, Moura CF, Caldeira MC et al (2006) Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. Plant Cell Environ 29:571–583. https://doi.org/10.1111/j.1365-3040.2005.01433.x

Mailly D, Kimmins JP, Busing RT (2000) Disturbance and succession in a coniferous forest of northwestern North America: simulations with DRYADES, a spatial gap model. Ecol Model 127:183–205. https://doi.org/10.1016/S0304-3800(99)00208-2

Marie G, Simioni G (2014) Extending the use of ecological models without sacrificing details: a generic and parsimonious meta-modelling approach. Methods Ecol Evol 5:934–943. https://doi.org/10.1111/2041-210X.12250

Maris V, Huneman P, Coreau A et al (2018) Prediction in ecology: promises, obstacles and clarifications. Oikos 127:171–183. https://doi.org/10.1111/oik.04655

Martínez-Vilalta J, Sala A, Asensio D et al (2016) Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. Ecol Monogr 86:495–516. https://doi.org/10.1002/ecm.1231

Martin-StPaul N, Delzon S, Cochard H (2017) Plant resistance to drought depends on timely stomatal closure. Ecol Lett 20:1437–1447. https://doi.org/10.1111/ele.12851

McDowell NG, Fisher RA, Xu C et al (2013) Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. New Phytol 200:304–321. https://doi.org/10.1111/nph.12465

McDowell NG, Williams AP, Xu C et al (2016) Multi-scale predictions of massive conifer mortality due to chronic temperature rise. Nat Clim Chang 6:295–300. https://doi.org/10.1038/NCLIMATE2873

Mina M, Martin-Benito D, Bugmann H, Cailleret M (2016) Forward modeling of tree-ring width improves simulation of forest growth responses to drought. Agric For Meteorol 221:13–33. https://doi.org/10.1016/j.agrformet.2016.02.005

Misson L, Rathgeber C, Guiot J (2004) Dendroecological analysis of climatic effects on Quercus petraea and Pinus halepensis radial growth using the process-based MAIDEN model. Can J Forest Res 34:888–898. https://doi.org/10.1139/x03-253

Moran EV, Ormond RA (2015) Simulating the interacting effects of intraspecific variation, disturbance, and competition on climate-driven range shifts in trees. PLoS One 10:1–21. https://doi.org/10.1371/journal.pone.0142369

Moran EV, Hartig F, Bell DM (2016) Intraspecific trait variation across scales: implications for understanding global change responses. Glob Chang Biol 22:137–150. https://doi.org/10.1111/gcb.13000

Morán-Ordóñez A, Roces-Díaz JV, Otsu K, Ameztegui A, Coll L, Lefevre F, Retana J, Brotons L (2019) The use of scenarios and models to evaluate the future of nature values and ecosystem services in Mediterranean forests. Reg Environ Chang 19:415–428. https://doi.org/10.1007/s10113-018-1408-5

Moriondo M, Good P, Durao R, Bindi M, Giannakopoulos C, Corte-Real J (2006) Potential impact of climate change on fire risk in the Mediterranean area. Clim Res 31:85–95. https://doi.org/10.3354/cr031085

Mouquet N, Lagadeuc Y, Devictor V et al (2015) Predictive ecology in a changing world. J Appl Ecol 52:1293–1310. https://doi.org/10.1111/1365-2664.12482

Nelson RM, Pettersson ME, Carlborg Ö (2013) A century after Fisher: time for a new paradigm in quantitative genetics. Trends Genet 29: 669–676. https://doi.org/10.1016/j.tig.2013.09.006

Obeso JR (1988) The costs of reproduction in plants. New Phytol 155: 321–348. https://doi.org/10.1046/j.1469-8137.2002.00477.x

Oddou-Muratorio S, Davi H (2014) Simulating local adaptation to climate of forest trees with a physio-demo-genetics model. Evol Appl 7:453–467. https://doi.org/10.1111/eva.12143

Oddou-Muratorio S, Gauzere J, Bontemps A, Rey JF, Klein EK (2018) Tree, sex and size: ecological determinants of male versus female fecundity in three Fagus sylvatica stands. Mol Ecol 27:3131–3145. https://doi.org/10.1111/mec.14770

Ogée J, Brunet Y, Loustau D et al (2003) MuSICA, a CO2, water and energy multilayer, multileaf pine forest model: evaluation from hourly to yearly time scales and sensitivity analysis. Glob Chang Biol 9:697–717. https://doi.org/10.1046/j.1365-2486.2003.00628.x

Pastorello GZ, Papale D, Chu H, Trotta C, Agarwal D, Canfora E, Baldocchi D, Torn M (2017) A new data set monitors land-air exchanges. Eos 98:27–32. https://doi.org/10.1029/2017eo071597

Pelletier F, Clutton-Brock T, Pemberton J et al (2007) The evolutionary demography of ecological change: linking trait variation and population growth. Science 315:1571–1574. https://doi.org/10.1126/science.1139024

Pemberton JM (2008) Wild pedigrees: the way forward. Proc R Soc B Biol Sci 275:613–621. https://doi.org/10.1098/rspb.2007.1531

Piou C, Prévost E (2013) Contrasting effects of climate change in continental vs. oceanic environments on population persistence and microevolution of Atlantic salmon. Glob Chang Biol 19:711–723. https://doi.org/10.1111/gcb.12085

Piou C, Berger U, Grimm V (2009) Proposing an information criterion for individual-based models developed in a pattern-oriented modelling framework. Ecol Model 220:1957–1967. https://doi.org/10.1016/j.ecolmodel.2009.05.003

Pitelka LF, Bugmann H, Reynolds JF (2001) How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Climatic Change 51:251–257. https://doi.org/10.1023/A:1012501409429

Polechová J, Barton N, Marion G (2009) Species' range: adaptation in space and time. Rhe Am Natural 174:E186–E204. https://doi.org/10.1086/605958

Poorter L, Wright SJ, Paz H et al (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. Ecology 89:1908–1920. https://doi.org/10.1890/07-0207.1

Porté A, Bartelink HH (2002) Modelling mixed forest growth: a review of models for forest management. Ecol Model 150:141–188. https://doi.org/10.1016/S0304-3800(01)00476-8

Pretzsch H, Forrester DI, Rötzer T (2015) Representation of species mixing in forest growth models: a review and perspective. Ecol Model 313:276–292. https://doi.org/10.1016/j.ecolmodel.2015.06.044

Quinn Thomas R, Canham CD, Weathers KC, Goodale CL (2010) Increased tree carbon storage in response to nitrogen deposition in the US. Nat Geosci 3:13–17. https://doi.org/10.1038/ngeo721

Rudman SM, Barbour MA, Csilléry K et al (2018) What genomic data can reveal about eco-evolutionary dynamics. Nature Ecol Evol 2:9–15. https://doi.org/10.1038/s41559-017-0385-2

Rykiel EJ (1996) Testing ecological models: the meaning of validation. Ecol Model 90:229–244. https://doi.org/10.1016/0304-3800(95)00152-2

Sakschewski B, von Bloh W, Boit A, et al. (2016) Resilience of Amazon forests emerges from plant trait diversity. Nature climate change 6:1032−+. https://doi.org/10.1038/NCLIMATE3109

Scheller RM, Mladenoff DJ, Crow TR, Sickley TA (2005) Simulating the effects of fire reintroduction versus continued fire absence on forest composition and landscape structure in the boundary waters canoe area, northern Minnesota, USA. Ecosystems 8:396–411. https://doi.org/10.1007/s10021-003-0087-2

Sebbenn AM, Degen B, Azevedo VCR, Silva MB, de Lacerda AEB, Ciampi AY, Kanashiro M, Carneiro FS, Thompson I, Loveless MD (2008) Modelling the long-term impacts of selective logging on genetic diversity and demographic structure of four tropical tree species in the Amazon forest. For Ecol Manag 254:335–349. https://doi.org/10.1016/j.foreco.2007.08.009

Seidl R, Rammer W, Scheller RM, Spies TA (2012) An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol Model 231:87–100. https://doi.org/10.1016/j.ecolmodel.2012.02.015

Simioni G, Le Roux X, Gignoux J, Sinoquet H (2000) Treegrass: a 3D, process-based model for simulating plant interactions in tree-grass ecosystems. Ecol Model 131:47–63. https://doi.org/10.1016/S0304-3800(00)00243-X

Soularue J-P, Kremer A (2012) Assortative mating and gene flow generate clinal phenological variation in trees. BMC Evol Biol 12:79. https://doi.org/10.1186/1471-2148-12-79

Soularue J-P, Kremer A (2014) Evolutionary responses of tree phenology to the combined effects of assortative mating, gene flow and divergent selection. Heredity 113:485–494

Takeuchi Y, Innan H (2015) Evaluating the performance of neutrality tests of a local community using a niche-structured simulation model. Oikos 124:1203–1214. https://doi.org/10.1111/oik.01703

Talkkari A, Kellomäki S, Peltola H (1999) Bridging a gap between a gap model and a physiological model for calculating the effect of temperature on forest growth under boreal conditions. For Ecol Manag 119:137–150. https://doi.org/10.1016/S0378-1127(98)00518-0

Vacchiano G, Ascoli D, Berzaghi F, Lucas-Borja ME, Caignard T, Collalti A et al (2018) Reproducing reproduction: how to simulate mast seeding in forest models. Ecol Model 376:40–53. https://doi.org/10.1016/j.ecolmodel.2018.03.004

Vinson CC, Kanashiro M, Sebbenn AM, Williams TCR, Harris SA, Boshier DH (2015) Long-term impacts of selective logging on two Amazonian tree species with contrasting ecological and reproductive characteristics: inferences from eco-gene model simulations. Heredity (Edinb) 115:130–139. https://doi.org/10.1038/hdy.2013.146

Visser MD, Bruijning M, Wright SJ et al (2016) Functional traits as predictors of vital rates across the life cycle of tropical trees. Funct Ecol 30:168–180. https://doi.org/10.1111/1365-2435.12621

Walker AP, Aranda I, Beckerman AP, Bown H, Cernusak LA, Dang QL, Domingues TF, Gu L, Guo S, Han Q, Kattge J, Kubiske M, Manter D, Merilo E, Midgley G, Porte A, Scales JC, Tissue D, Turnbull T, Warren C, Wohlfahrt G, Woodward FI, Wullschleger SD (2014) A global data set of leaf photosynthetic rates, leaf N and P, and specific leaf area. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ORNLDAAC/1224

Weng ES, Malyshev S, Lichstein JW, Farrior CE, Dybzinski R, Zhang T, Shevliakova E, Pacala SW (2015) Scaling from individual trees to forests in an earth system modeling framework using a mathematically tractable model of height-structured competition. Biogeosciences 12:2655–2694. https://doi.org/10.5194/bg-12-2655-2015

Weng E, Farrior CE, Dybzinski R, Pacala SW (2017) Predicting vegetation type through physiological and environmental interactions with leaf traits: evergreen and deciduous forests in an earth system modeling framework. Glob Chang Biol 23:2482–2498. https://doi.org/10.1111/gcb.13542

Wernsdörfer H, Caron H, Gerber S, Cornu G, Rossi V, Mortier F, Gourlet-Fleury S (2011) Relationships between demography and gene flow and their importance for the conservation of tree populations in tropical forests under selective felling regimes. Conserv Genet 12:15–29. https://doi.org/10.1007/s10592-009-9983-0

Yousefpour R, Jacobsen JB, Thorsen BJ, Meilby H, Hanewinkel M, Oehler K (2012) A review of decision-making approaches to handle uncertainty and risk in adaptive forest management under climate change. Ann For Sci 69:1–15. https://doi.org/10.1007/s13595-011-0153-4

Zhao M, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329:940–943. https://doi.org/10.1126/science.1189590

Zhao S, Pederson N, D'Orangeville L et al (2019) The International Tree-Ring Data Bank (ITRDB) revisited: data availability and global ecological representativity. J Biogeogr 46:355–368. https://doi.org/10.1111/jbi.13488

Zuidema PA, Franco M (2001) Integrating vital rate variability into perturbation analysis: an evaluation for matrix population models of six plant species. J Ecol 89:995–1005. https://doi.org/10.1046/j.0022-0477.2001.00621