

# Modeling forest growth under climate change

Issam Boukhris<sup>1</sup>, Gina Marano<sup>1</sup>, Daniela Dalmonech<sup>1</sup>, Riccardo Valentini<sup>1</sup>, and Alessio Collalti<sup>1</sup>

<sup>1</sup>Affiliation not available

November 26, 2024

## Abstract

### *Purpose of Review*

Forests are integral to global ecological stability, climate regulation, and economic resilience. They function as major carbon sinks, act as biodiversity reservoirs, and provide ecosystem services. Accurately modeling forest growth is essential to predict ecosystem responses to climate change and optimize ecosystem services. However, predicting forest growth remains challenging due to complex interactions between ecological processes, external drivers like climate change, and intrinsic dynamics, such as legacy effects and emergent properties, that influence forest responses over time.

This work offers a detailed examination of theories in forest growth modeling, with a focus on emergent approaches as implemented in 18 forest growth models, which vary in their approaches and goals.

### *Recent Findings*

Forest modeling requires a deep understanding of forest growth theories driven by multiple, often interacting, processes. Our findings reveal distinct model clusters with varying process integrations and complexity, ranging from stand-level to terrestrial ecosystem models. Additionally, we highlight the trade-offs between model detail and scalability.

### *Summary*

Our review showcases multiple theories, such as Functional Balance, Local Determination of Growth, and Optimality Principles of forest growth, thus providing a synthetic overview of the main frameworks for resource allocation in plants. As multiple studies emphasize the importance of integrating different and recent theories to better capture growth dynamics, we build on a state-of-the-art multi-modelling comparison to discuss what the implications of different theories might be at different temporal and spatial resolutions. Finally, we explore how emerging technologies, such as machine learning, can enhance predictive accuracy and help address current modeling limitations.

# Modeling forest growth under climate change

**Authors:** Boukhris I.<sup>1,2,†</sup>, Marano G.<sup>3,4,†</sup>, Dalmonech D.<sup>4,5</sup>, Valentini R.<sup>1,2</sup>, Collalti A.<sup>4,5,\*</sup>

## **Affiliations:**

1. Department for Innovation in Biological, Agri-Food and Forest Systems (DIBAF), University of Tuscia, 01100 Viterbo, Italy

2. CMCC Foundation - Euro-Mediterranean Center on Climate Change, Italy

3. Department of Environmental Systems Science, Forest Ecology, Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland

4. Forest Modeling Lab, Institute for Agriculture and Forestry Systems in the Mediterranean, National Research Council of Italy (CNR-ISAFOM), 06128 Perugia, Italy

5. National Biodiversity Future Center (NBFC), 90133 Palermo, Italy

† contributed equally

\***Corresponding author:** [alessio.collalti@cnr.it](mailto:alessio.collalti@cnr.it)

## **Abstract**

### *Purpose of Review*

Forests are integral to global ecological stability, climate regulation, and economic resilience. They function as major carbon sinks, act as biodiversity reservoirs, and provide ecosystem services. Accurately modeling forest growth is essential to predict ecosystem responses to climate change and optimize ecosystem services. However, predicting forest growth remains challenging due to complex interactions between ecological processes, external drivers like climate change, and intrinsic dynamics, such as legacy effects and emergent properties, that influence forest responses over time.

This work offers a detailed examination of theories in forest growth modeling, with a focus on emergent approaches as implemented in 18 forest growth models, which vary in their approaches and goals.

30 *Recent Findings*

31 Forest modeling requires a deep understanding of forest growth theories driven by multiple,  
32 often interacting, processes. Our findings reveal distinct model clusters with varying process  
33 integrations and complexity, ranging from stand-level to terrestrial ecosystem models.  
34 Additionally, we highlight the trade-offs between model detail and scalability.

35 *Summary*

36 Our review showcases multiple theories, such as Functional Balance, Local Determination of  
37 Growth, and Optimality Principles of forest growth, thus providing a synthetic overview of  
38 the main frameworks for resource allocation in plants. As multiple studies emphasize the  
39 importance of integrating different and recent theories to better capture growth dynamics, we  
40 build on a state-of-the-art multi-modelling comparison to discuss what the implications of  
41 different theories might be at different temporal and spatial resolutions. Finally, we explore  
42 how emerging technologies, such as machine learning, can enhance predictive accuracy and  
43 help address current modeling limitations.

44

## 45 **1. Introduction**

46 Forests are pivotal in maintaining global ecological stability, ensuring economic security, and  
47 regulating climate systems. They act as potential carbon sinks, support biodiversity, and  
48 provide essential resources and services that sustain human and environmental well-being  
49 (1,2). Understanding forest growth extends beyond basic ecological interest: it encompasses  
50 economic, environmental, and social dimensions, as forests not only contribute to  
51 biodiversity and serve as carbon sinks but also protect against natural calamities and support  
52 multiple ecosystem functionalities (3,4). Changes in forest growth patterns serve as indicators  
53 of forest health and potential ecological shifts, influence legacy effects, and help managing  
54 disturbances (5). Thus, predicting these changes with high accuracy is imperative for reliably  
55 studying future trajectories of forest dynamics and ecosystem functioning under climate  
56 change (6,7). However, the ability of process-based models to accurately predict forest  
57 growth has become increasingly challenging due to the intricate interplay of ecological  
58 processes and the external factors that influence forest dynamics, particularly in the context  
59 of climate change (8–10). Accurate process representation is critical for trustworthy  
60 predictions, yet it is often hindered by the, still limited, understanding of key ecological  
61 interactions and feedback (11,12).

62 Emergent and unpredictable patterns further complicate growth modeling as they arise when  
63 multiple processes interact in unforeseen ways, leading to outcomes that cannot be easily  
64 inferred by simply summing up individual effects. This complexity challenges the analysis of  
65 forest growth sensitivity to climate change and underscores the need for a holistic modeling  
66 approach (13,14). Early warning signals, crucial for anticipating transitions in forest health  
67 and productivity (15–17), are often difficult to detect due to the subtle, nonlinear, and delayed  
68 responses of forest ecosystems to stressors (18,19). Additionally, legacy effects — long-  
69 lasting impacts of past climatic events, environmental conditions, or human interventions —

70 add significant complexity to forest dynamics by influencing growth, resilience and recovery  
71 through feedback loops (20–23). Climate-induced alterations, such as increasing  
72 temperatures, changing precipitation patterns, and extreme weather events, can unpredictably  
73 modify growth patterns, complicating the use of historical data for future predictions (7,9,24).  
74 Despite such limitations, the scientific community offers a plethora of forest/vegetation  
75 models, differing in assumptions and thus process implementation, which results in a  
76 multitude of projections (see e.g., 25–28).

77 Currently, there is a tendency to promote highly mechanistically-based forest growth models  
78 as several studies claim that they offer distinct advantages in predicting forest growth, thanks  
79 to their foundation in conservation laws, monotonicity, and feedback mechanisms. These  
80 features contribute to robust predictions in the context of non-stationary climate and changing  
81 environmental regimes (29,30), as they are built on causal relationships, enabling them to  
82 answer effectively to many scientific questions (9,31). Several studies have however proven  
83 that despite the inherent process complexity, often the highly mechanistic models fail to  
84 reproduce the most recent trends in growth decline and associated disturbance and climatic-  
85 extreme related mortalities (32–34), thus highlighting the need to carefully consider  
86 alternative modeling theories and process implementation in vegetations models.

87 This work provides a perspective on the consolidated and emergent theories for the last  
88 decades and the evolution of forest growth approaches as implemented in a suite of 18,  
89 different in nature, as representatives of the available forest growth models while  
90 emphasizing the integration of theoretical paradigms and empirical data to enhance predictive  
91 accuracy under climate change trajectories and increasing uncertainty. Furthermore, the paper  
92 discusses the potential of emerging technologies such as the ones based on machine learning,  
93 and interdisciplinary approaches in overcoming these challenges highlighting significant  
94 opportunities for advancing forest growth predictions.

95 This review is structured as follows: **Section 2** overviews key grounding theories in forest  
96 growth modeling, examining both foundational and contemporary approaches to growth  
97 regulation at the tree level. **Section 3** analyzes various modeling approaches, detailing how  
98 different models represent growth dynamics, mortality, and regeneration across spatial and  
99 temporal scales. **Section 4** considers the implications of these theories for model selection,  
100 assessing trade-offs in complexity, scalability, and ecological accuracy. **Section 5** addresses  
101 current challenges and limitations, including data constraints, computational demands, and  
102 gaps in knowledge of specific processes. **Section 6** concludes with future directions, focusing  
103 on the potential for integrating machine learning with forest models to improve predictive  
104 accuracy, adaptability, and ecological insights under climate change. Definition of words is  
105 based on the glossary provided in the Glossary 1.

## 106 **2. Theories of Forest Growth**

107 Growth refers to the physiological process by which organs, single pools, entire plants or  
108 communities increase their biomass because of increases in cell number, driven by the highly  
109 coordinated activities of cell division, expansion and differentiation and their death (35). In  
110 trees, growth is typically measured by the increment of the stem in volume, diameter, or tree  
111 height with the growth rate often equated to the accumulated biomass at a given time (36).  
112 Plant growth follows, in principle, an exponentially increasing curve which persists until the  
113 plant's death (37). Under optimal environmental conditions, the rate of biomass accumulation  
114 in trees increases continuously with tree size and the relative growth rate can peak at  
115 approximately  $1 \text{ g g}^{-1} \text{ week}^{-1}$  meaning the plant's size could potentially double within a week  
116 (38). However, at a relatively coarse spatial scale (e.g., stand and landscape), the net growth  
117 concept is used, which considers not only the growth of e.g. single pools or individual trees  
118 but also includes mortality (tree death) and recruitment (ingrowth).

119 Growth in plants results from the inherently complex balance between the supply and the  
120 demand of carbohydrate and nutrient substrates. This process is driven by feedback  
121 mechanisms between supply and demand, making allocation a property of a system that  
122 encompasses several distinct processes (39,40).

123 The development of forest growth models has historically been significantly influenced by  
124 competing theories that focus on different aspects of forest ecology. For instance, the  
125 '*Functional Balance*' theory refers to the equilibrium between the supply of resources for  
126 growth and the need for proper functioning of plant tissues (41) and establishes a balance  
127 between leaf and root activities. Changes in environmental factors or interventions like  
128 pruning can disturb the functional balance, but plants generally respond by reallocating  
129 resources to minimize limitations to growth (40,42).

130 According to the '*Local Determination of Growth*' theory, growth patterns in plants are  
131 adapted to optimize resource capture (43). This adaptation promotes efficient resource  
132 capture by favoring the growth of parts of the plant that acquire limiting resources.

133 The '*Optimality Principles*' theory suggests instead that resource allocation is driven by long-  
134 term evolutionary trends and immediate short-term responses to seasonal physiological and  
135 metabolic adjustments to environmental changes, which can influence their growth, survival  
136 and reproduction (44). Lastly, the '*Coordination*' theory proposes that growth is regulated by  
137 the balance between distinct processes, coordinated by an internal mechanism in response to  
138 changing external conditions. While focusing on immediate regulation, this theory does not  
139 necessarily exclude the possibility that these mechanisms are aligned with broader  
140 evolutionary and adaptability goals (40).

141 In the realm of growth modeling applied to trees, two main general approaches can be  
142 recognized which are built on '*photosynthetic*' and '*non-photosynthetic*' growth process  
143 representation (30,45) (Figure 1).

144 At the center of the '*photosynthetic-centric*' approach, the photosynthesis process controls  
145 growth with growth resulting from the net balance between synthesized sugars and those lost  
146 because of metabolic activity (i.e. autotrophic respiration). Ultimately, growth is considered  
147 as the result of photosynthesis less the metabolic costs for synthesizing new tissues (growth  
148 respiration) and for maintaining the existing ones (maintenance respiration; the well-known  
149 '*Growth and Maintenance Respiration Paradigm*', GMRP; (46,47)) and the portion of non-  
150 structural carbon (NSC) not used for biomass growth including sugars to mycorrhizas and  
151 biogenic volatile organic compounds (48–50). These processes result in the synthesis of new  
152 biomass and can be significantly influenced by environmental conditions such as  
153 temperature, light, wind, and nutrient and water availability. The photosynthetic-centric  
154 approach is adopted by models like: 3-PG (51), 3D-CMCC-FEM (52,53), GOTILWA+ (54)  
155 4C (55), LANDIS (56), iLand (57), LPJ-GUESS 4.0 (58), GO+ (59), SEIB-DGVM (60),  
156 FATES (61), HYBRID 4.0 (62) ED (63), and aDGVM (64).

157 At the leaf or canopy level, there are two main and common approaches to model  
158 photosynthesis: a) the Light Use Efficiency (LUE) approach, which empirically estimates  
159 photosynthesis based on the efficiency of converting absorbed light into biomass (65); and, b)  
160 the biochemical model of Farquhar, von Caemmerer, and Berry (66), which mechanistically  
161 incorporates factors like Rubisco activity and atmospheric and intercellular CO<sub>2</sub>  
162 concentration (67).

163 Historically, most of the models integrated the sole photosynthetic-centric approach (both as  
164 LUE or FvCB or intermediate versions of these two) emphasizing the source side, where  
165 growth is viewed as a direct result of the carbon assimilated through photosynthesis. Theories  
166 like the '*Functional Balance*' and '*Local Determination of Growth*' imply that without a  
167 sufficient supply of photosynthetic products, growth cannot proceed efficiently, thus placing  
168 the source at the forefront of the growth process.



169 In contrast to the photosynthetic-centric approach, which primarily focuses on source-driven  
170 models that emphasize the supply of carbon and nutrients as the key drivers of plant growth,  
171 the '*non-photosynthetic-centric*' approach offers a more nuanced understanding by  
172 incorporating source-sink dynamics (30). This perspective recognizes that plant growth is not  
173 solely determined by the availability of resources (such as atmospheric CO<sub>2</sub>, water and soil  
174 nutrients), but also by the critical role of sink strength in regulating photosynthesis and  
175 biomass allocation, particularly under varying environmental conditions (68). This approach  
176 moves beyond simple carbon balance models by acknowledging that plants actively manage  
177 resource acquisition and allocation between different organs (e.g. leaves, stems and roots)  
178 based on both immediate physiological demands and long-term survival strategies (30,68–  
179 72). Non-photosynthesis-centric models such as ForClim and LandClim fall into this  
180 category, as they do not simulate photosynthesis directly. Instead, population dynamics are  
181 governed by 'growth,' which is calculated without explicitly modeling the photosynthetic  
182 process. These models account for physiological limits and the demand of various organs  
183 (sinks) in regulating growth, especially under stress conditions via empirical relationships.  
184 For example, ForClim operates at a lower complexity level, with simpler carbon allocation  
185 mechanisms. However, these models are well-suited for capturing long-term forest dynamics  
186 in stands or landscapes where resource limitations, such as water or nutrients, play a  
187 significant role.

188 As an underlying theory to the *non-photosynthetic centric* approach, the *Optimality theory*  
189 posits that plants optimize resource allocation to maximize net carbon gain while minimizing  
190 physiological costs associated with photosynthesis and hydraulic maintenance (73). In this  
191 perspective, plants optimize their growth by balancing the needs of these sinks with the  
192 resources available, thereby implying that the sink could be the primary driver (45,74).

193 This involves balancing trade-offs among carbon assimilation, water-use efficiency, and the  
194 risk of hydraulic failure due to xylem embolism (75–77). In addition, recent studies highlight  
195 how plants are optimizing agents that allocate resources to maximize long-term fitness  
196 through strategic investments enhancing future resource capture, stress resilience, and  
197 competitiveness. By incorporating economic principles into ecological modeling, the  
198 maximum optimization provides a novel perspective on plant resource allocation strategies  
199 under fluctuating environmental conditions (78,79). This theory brings the sink into focus,  
200 suggesting that the demand from various plant tissues (sinks) for resources is what,  
201 ultimately, drives growth.

202 The integration of the two primary approaches — photosynthetic-centric and non-  
203 photosynthetic-centric — highlights a fundamental conceptual challenge that resembles the  
204 classic "chicken-and-egg" dilemma. In the context of plant growth, this dilemma raises the  
205 question: which comes first, the source (photosynthesis and carbon supply) or the sink (the  
206 demand from growing tissues)?

207 This interplay between source and sink dynamics is not merely academic — it is crucial for  
208 developing accurate models of plant growth. Just as the chicken-and-egg question forces us to  
209 consider the origin of life cycles, these growth theories compel us to rethink the starting point  
210 of the growth process: is it the photosynthetic carbon supply (the "egg") that initiates growth,  
211 or is it the demand from growing tissues (the "chicken") that governs how resources are  
212 allocated, and growth is achieved? This debate is central to understanding plant growth  
213 because it forces us to consider whether it is the availability of resources (like carbon from  
214 photosynthesis) that primarily drives growth, or if it is the capacity of plant tissues to utilize  
215 these resources (the sinks) that governs how resources are allocated and ultimately, how  
216 growth occurs (80).

### 217 **3. Approaches to Model Growth in Forest Models**

218 Models simulate forest growth through diversified approaches, each designed to capture  
219 distinct aspects of growth dynamics. For instance, dynamic global vegetation models  
220 (DGVMs) like LPJ-GUESS and SEIB-DGVM focus on global scale simulations by  
221 incorporating large-scale climate-vegetation feedback and disturbances regimes, often  
222 emphasizing biogeographical shifts across ecosystems and climate zones. Stand models that  
223 belong to the forest succession gap model family, such as FORMIND (81) and ForClim (82)  
224 focus on the simulation of forest dynamics by modeling the establishment, growth, and  
225 mortality of individual trees or small patches of forest, emphasizing the effects of species-  
226 specific traits and light-competition on growth patterns.

227 Stand-level models like 3-PG, 3D-CMCC-FEM and 4C offer a detailed mechanistic  
228 representation of tree growth by simulating the interaction between tree physiology and  
229 environmental variables at the single tree level and then extrapolate that at the landscape  
230 scale, often focusing on a single species.

231 These models vary significantly in their complexity, spatial and temporal scales, and the  
232 specific growth attributes they emphasize, such as stem diameter, height, productivity, or  
233 overall biomass accumulation, as well as important processes like mortality and recruitment,  
234 which together shape long-term forest dynamics. Each model comes with different degrees of  
235 empiricism or mechanism that employ different theories (as the ones described in the  
236 previous section) and methodologies to model forest growth.

237 In this section, process-based models were thus analyzed in more detail, in terms of their  
238 ability to simulate key components and subcomponents of forest growth, which are critical  
239 for understanding forest dynamics under various environmental and management conditions  
240 to discern patterns in model design and functionality across different scales (stand, landscape,  
241 terrestrial ecosystem) and to understand how these models align with specific research and

242 management objectives. The components include aspects such as model structure, temporal  
243 and spatial resolution, mortality processes, and allocation mechanisms, among others (Table  
244 1). Our work is inspired by the dataset of process-based models by (83), highlighting the  
245 various integrations of theoretical approaches to model forest growth and the impacts of  
246 climate change. We reviewed a total of 18 well-documented models, ensuring a  
247 representative sample that spans a variety of different modeling approaches (Table S1). The  
248 criteria used to categorize these models, as shown in Table 2, include Spatial Scale, Temporal  
249 Resolution, Growth Processes, Mortality and Establishment.

250 We conducted a hierarchical clustering based on the complexity of their modalities  
251 corresponding to specific traits (Tables 2-3). The complexity of each trait's modality was  
252 assessed ordinally, focusing on both structural components and functional processes. The  
253 results of this clustering are presented in Figure 2.

254 The final clustering is based on the complexity of various traits and modalities, which  
255 represent the structural and functional components that each model employs to simulate  
256 forest growth. The cluster map uses a color gradient to indicate the complexity of each trait  
257 within the models, with darker colors corresponding to higher complexity levels.

258 The cluster map reveals three major clusters (See Figure 3), which correspond to different  
259 levels of model complexity and operational scales.

260 The cluster map not only categorizes the models based on complexity but also highlights the  
261 relationships between different traits and their influence on model functionality. For example,  
262 there is a clear correlation between the temporal and spatial resolution of a model and its  
263 overall complexity. Models with finer temporal resolution (e.g., daily updates) tend to have  
264 higher complexity in modelling forest growth and are more likely to include dynamic  
265 environmental interactions (e.g., LPJ-GUESS 4.0 and 3D-CMCC-FEM). Similarly, models  
266 that operate at larger spatial scales (e.g., global) require mechanisms to simulate broader

267 ecosystem dynamics (e.g., CLM-FATES and SEIB-DGVM). Models that include detailed  
268 mortality processes, particularly those that account for stress and disturbance, are often more  
269 complex and integrated with dynamic allocation processes. Importantly, the approach to  
270 modeling photosynthesis significantly influences the model's complexity and the modeling of  
271 growth. Models that use mechanistic photosynthesis models are generally more complex, as  
272 they require detailed input on environmental variables and a higher number of parameters  
273 (e.g., GO+ 3.0, 3D-CMCC-FEM, FATES, LPJ-GUESS 4.0).

274       • 3.1. Cluster 1: stand-scale models

275 This cluster predominantly comprises stand-scale models that focus on localized, highly  
276 detailed stand-level processes and forest dynamics. Operating at a single stand level with  
277 minimal spatial complexity, these models emphasize individual tree or cohort growth. They  
278 typically employ high temporal resolutions, using daily or sub-daily time steps to update tree  
279 productivity, thereby capturing short-term variability over time; however, some forest gap  
280 models operate on an annual time step. The approaches to photosynthesis modeling within  
281 this cluster are diverse — ranging from empirical and semi-empirical to mechanistic methods  
282 — resulting in varying levels of complexity across different models. Notably, these models  
283 often include multi-species dynamics, enabling more accurate simulations of species  
284 competition and succession in mixed forests (e.g., 3PGmix, 4C, and 3D-CMCC-FEM).  
285 Mortality processes are frequently static, characterized by fixed background mortality rates  
286 that do not dynamically respond to environmental stresses or disturbances (e.g., 3PG and  
287 FOREST-BGC). Additionally, natural regeneration is generally not accounted for as an  
288 independent process; at best, these models incorporate prescribed recruitment (e.g., (83);  
289 CASTANEA (84) and SPA, (85). Consequently, while these traits render the models efficient  
290 for specific, more intricate forest management scenarios — such as predicting growth in

291 uniform or heterogeneous stands under stable or varying environmental conditions — their  
292 spatial simplicity limits their applicability in geographically complex and heterogeneous  
293 forest ecosystems (86–89). They typically lack integration of broad-scale environmental  
294 processes and feedback mechanisms (e.g., hydrological cycles and disturbance regimes)  
295 between the forest ecosystem and its surrounding environment.

296 • 3.2. Cluster 2: landscape-scale models

297 This cluster encompasses models that generally operate at the landscape scale, incorporating  
298 a lower degree of spatial and temporal resolution compared to stand models, which makes  
299 them suitable for simulating complex interactions across larger and more heterogeneous  
300 forested areas. These models often include multi-species dynamics, allowing for more  
301 accurate simulations of species competition and succession in mixed forests (e.g., TreeMig,  
302 (90); and iLand, (91)). They frequently employ monthly or sub-monthly time steps for  
303 environmental variables such as temperature and soil moisture, facilitating straightforward  
304 projections. Unlike the models in Cluster 1, they include disturbance-related mortality  
305 mechanisms in response to factors like drought, pests, landslides, and wildfires; for instance,  
306 they can account for tree mortality caused by high-severity wildfires or simulate tree death  
307 triggered by landslides or avalanches in mountainous regions, accurately modeling observed  
308 mortality events (e.g., LandClim 2.0, ForClim 4.0.1, and FIRE-BGC, (92)). Additionally,  
309 these models explicitly represent the establishment process, allowing for the inclusion of  
310 demographic components (e.g., the LANDIS-II and ForCLim models, but see also (93)).  
311 However, they are characterized by a simplistic way of presenting the growth process, often  
312 relying on empirical approaches to represent growth. Overall, these models are well-suited  
313 for landscape-level analysis where interactions between different forest patches, species, and  
314 environmental conditions must be considered (e.g., LANDIS-II for simulating forest

315 succession and disturbance, and LandClim 2.0 for climate and wildfire interactions), striking  
316 a balance between complexity and usability, and making them effective tools for regional  
317 forest management and conservation planning.

318       • 3.3. Cluster 3: terrestrial ecosystem-scale models

319 The third cluster comprises models that operate at the terrestrial scale, characterized by high  
320 complexity due to their simulation of large-scale processes such as biome shifts, land-use  
321 changes, and long-term feedback between ecosystems and the global climate system —  
322 critical for understanding forest dynamics at larger spatial scales. These models often employ  
323 mechanistic approaches, integrating detailed process-based representations of photosynthesis,  
324 respiration, and growth alongside the biophysics of the system, as they are frequently used as  
325 boundary conditions for atmospheric models (e.g., the LPJ-GUESS and FATES models, but  
326 see also CLM, (94) and ORCHIDEE, (95)). This enables them to simulate complex  
327 interactions between biotic and abiotic factors across multiple spatial and temporal scales  
328 (96,97). Similar to the models in Cluster 1, they exhibit high sensitivity to climate variables  
329 like temperature and atmospheric CO<sub>2</sub> levels, incorporating sophisticated algorithms to  
330 simulate the impact of changing climate conditions on forest growth and carbon sequestration  
331 (e.g., see (98)). They utilize advanced carbon allocation theories, such as source-sink  
332 dynamics and optimality principles, to distribute carbon and nutrients within the ecosystem,  
333 allowing them to simulate how forests might shift growth strategies in response to  
334 environmental stressors. The allocation processes are dynamic, often incorporating feedback  
335 mechanisms that adjust growth allocation based on current environmental conditions and  
336 resource availability (see Table 1 in (99) for a comprehensive review on the carbon allocation  
337 strategies adopted by different models including those of the Cluster 3). Like the models in  
338 the second cluster, they account for dynamic disturbance-related mortality processes due to

339 factors such as fire, storms, and land-use change, enabling simulation of long-term impacts  
340 on global forest carbon balance and biodiversity (e.g., the HYBRID 4.0, ED, and aDGVM  
341 models). Operating at a global scale, these models incorporate data from various biomes and  
342 climate zones, making them highly versatile and computationally intensive. While designed  
343 for large-scale simulations focusing on broad processes like carbon cycling, nutrient  
344 dynamics, and carbon-climate feedback, they necessarily simplify species-specific  
345 parameterizations, resulting in the adoption of plant functional types rather than individual  
346 species. Despite this simplification, they provide critical insights into how forests worldwide  
347 will respond to different climate scenarios, aiding in the development of global  
348 environmental policies and strategies for carbon management.

#### 349 **4. Modeling Theories and Implications for Model Selection**

350 The complexity analysis of stand-, landscape-, and terrestrial ecosystem-scale models reveals  
351 distinct trade-offs between model detail, computational demands, and ecological processes  
352 represented.

353 Concerning the spatial scale of investigation, stand models are generally best suited for small-  
354 scale closed systems, where external agents (e.g., biotic disturbance agents) and spatial  
355 interactions across patches are not the primary focus. These models provide detailed growth  
356 simulations but often neglect crucial demographic processes like seed dispersal and process-  
357 based establishment routines, which are usually employed to analyze long-term stand  
358 dynamics and highlight their utility in long-term ecological forecasting (e.g. ForClim,  
359 FORMIND). At this spatial scale, however, modeling growth processes differs largely from  
360 strictly empirical to highly mechanistic approaches.

361 Models such as 3PG, 3D-CMCC-FEM, and 4C use various approaches to simulate  
362 photosynthesis, including the mechanistic FvCB model (66,100), the semi-empirical  
363 Haxeltine and Prentice model (96,101), and the empirical LUE model (102,103).



364 After accounting for the autotrophic respiration using either mechanistic representation (i.e.,  
365 the *GMRP* approach, (46,47), an empirically constrained fixed-ratio approach (104–107) or a  
366 mixed one (e.g., (108)), photosynthates are then allocated to different structural and non-  
367 structural tree biomass pools. Including photosynthesis representation in dynamic vegetation  
368 models enhances their capability to predict carbon fluxes comprehensively, but it also  
369 introduces trade-offs. The FvCB model provides mechanistic accuracy, capturing detailed  
370 responses to environmental changes at the cost of a high number of parameters to calibrate  
371 and increases uncertainty ranges, while the LUE approach offers computational simplicity  
372 suitable for large-scale, remotely-sensed driven, modeling applications. However, LUE can  
373 oversimplify critical processes, such as plant responses to stress at increasing temporal  
374 resolution and atmospheric CO<sub>2</sub> increases (the so-called ‘CO<sub>2</sub> fertilization effects’)

375 In contrast, landscape models, which offer a good balance between detail and utility, use  
376 more simplistic approaches for growth but effectively model demographic processes such as  
377 establishment and natural mortality, making them valuable tools for large-scale ecological  
378 assessments (109). They are particularly effective in heterogeneous landscapes where species  
379 interactions and environmental variability play significant roles.

380 Some of these models are not strictly centered on photosynthesis (e.g. TreeMig, LandClim),  
381 and use in most cases empirical response curves to simulate forest growth without accounting  
382 for the whole carbon balance of forest ecosystems which provides high efficiency in terms of  
383 computation costs and enhances the model application across large spatial extents, although  
384 results in coarser prediction in terms of tree growth (see Table 6 in (110) for a comprehensive  
385 cross-checking of the carbon balance by different models).

386 Ecosystem models, which are the result of integrative research efforts such as global climate  
387 modeling and policy development, are well-balanced in representing growth, mortality, and  
388 establishment, but their high computational costs limit their scalability and real-time

389 application. These models dynamically allocate photosynthates to different tree biomass  
390 pools, guided by first principles such as in the ‘Pipe model’, ‘Resource Limitation’, and  
391 ‘Functional Balance’, theories after accounting for growth and maintenance respiration, as  
392 well as non-structural carbon, which is estimated only by some models in this category (e.g.,  
393 LPJ-GUESS, SEIB-DGVM, and FATES) (see also (99)). This dynamic and responsive  
394 process representation enables these models to simulate growth in a highly complex and  
395 potentially more realistic manner.

396 Concerning the funding theories of forest growth modeling, the comparison between  
397 *photosynthetic-centric* and *non-photosynthetic-centric* approaches in forest growth modeling  
398 is reflected in the traits and modalities presented in Table 2 and the hierarchical clustering  
399 shown in Figure 2. Despite the scale at which DVMs are employed, photosynthetic-centric  
400 models, such as 3D-CMCC-FEM (stand) and LPJ-GUESS (global and landscape), focus on  
401 carbon assimilation through photosynthesis as the primary driver of growth. In Figure 2,  
402 models in Cluster 3, such as LPJ-GUESS and SEIB-DGVM, are characterized by high  
403 complexity, dynamic carbon allocation processes, and high climate sensitivity. These models  
404 are apt to predict growth under fluctuating environmental conditions by capturing the  
405 intricate interactions between photosynthesis, plants’ respiration, carbon allocation, and  
406 environmental factors. However, a key limitation of these models is their high computational  
407 demand and potential oversimplification of sink dynamics, which may limit their ability to  
408 simulate responses under severe stress conditions, such as drought.

#### 409 **5. Current challenges and limitations in forest models**

410 Forest and terrestrial ecosystem models are essential tools in ecological modeling but  
411 encounter significant challenges under climate change scenarios. These models frequently  
412 fail to accurately predict growth in very heterogeneous environments (111,112) and detect  
413 subtle or abrupt ecological shifts preceding major transitions due to their reliance on average

414 conditions and deterministic equations, which obscure fine-scale variability, feedback loops,  
415 and legacy effects. Consequently, they may miss early warning signs of ecosystem changes,  
416 diminishing their utility in anticipating and mitigating adverse outcomes (15). Additionally,  
417 historical environmental conditions and past management actions, which critically influence  
418 current and future forest dynamics, are often underrepresented because of their complexity  
419 and the scarcity of comprehensive historical data. Accurately capturing these legacy effects  
420 necessitates more sophisticated and computationally intensive model structures. The  
421 application of emergent constraints, which establishes explainable relationships between  
422 current modeled and observable variables and predicted outcomes, has successfully reduced  
423 uncertainties in climate models. However, when applied to vegetation and forest models, this  
424 approach assumes that these relationships remain stable over time, potentially  
425 underestimating novel climate dynamics and ecological feedback. Moreover, the limited  
426 availability and quality of observational data across different biomes can skew future  
427 projections, while the tendency to overfit models to present-day patterns may neglect outlier  
428 scenarios and unprecedented ecosystem shifts (113). Furthermore, theoretical frameworks  
429 such as ‘*Optimality*’ theory, which suggests that organisms adapt to maximize specific  
430 benefits like energy or resource use efficiency, often do not align with empirical observations  
431 (114–117). This discrepancy arises from multiple, conflicting constraints faced by organisms,  
432 phenotypic plasticity, environmental variability, and biological and evolutionary limitations,  
433 leading to suboptimal behavior in models. Plants must balance various demands, adjust  
434 dynamically to changing conditions, and operate under non-equilibrium dynamics, all of  
435 which challenge the strict predictions of optimality-based models. Additionally, unmeasured  
436 or misunderstood factors, such as nutrient limitations and root interactions, further complicate  
437 the accurate representation of plant behavior (118,119). In summary, while forest growth  
438 models are invaluable for understanding ecosystem dynamics, their limitations under climate

439 change stem from difficulties in detecting ecological shifts, inadequately representing legacy  
440 effects, the pitfalls of emergent constraints, and the complexities of implementing theoretical  
441 frameworks like ‘*Optimality*’ theory (13,120,121). Addressing these challenges requires  
442 integrating fine-scale variability, comprehensive historical data, cautious application of  
443 emergent constraints, and accommodating the complex, adaptive, and non-equilibrium nature  
444 of ecosystems within the models.

445 **6. Way forward and new opportunities with potential integration of Machine Learning**  
446 **with forest models.**

447 To address the challenges outlined in Section 5, we propose a comprehensive framework that  
448 enhances forest growth models through three key improvements: advancing biogeochemical  
449 process representation, optimizing parameter calibration, and enriching observational  
450 datasets. Current models are constrained by reliance on detailed site- and species-specific  
451 parameters (Cluster 1), high computational demands for large-scale applications (Cluster 2),  
452 inflexibility due to stringent assumptions (Cluster 3), and complex calibration processes  
453 (122,123). Our framework mitigates these limitations by leveraging advancements in  
454 computational capabilities and integrating artificial intelligence (AI). By combining  
455 mechanistic and machine learning (ML) approaches, we enhance predictive accuracy and  
456 robustness, utilizing ML’s flexibility despite its requirements for extensive datasets and  
457 challenges in explainability and extrapolation under stochastic conditions (124). We integrate  
458 legacy effects and advanced theoretical frameworks, such as ‘*Optimality*’ theory, with ML  
459 techniques to better capture complex ecological processes, enabling AI-driven models to  
460 adapt continuously through learning from extensive datasets and real-time feedback. Modular  
461 coupling allows ML to train sub-models within forest models, improving predictions of  
462 species migration in models like TreeMig and aDGVM (125,126). Innovative calibration  
463 methods, including real-time adaptive calibration and multi-objective optimization, utilize

464 high-resolution remote sensing data and ML to enhance parameter accuracy and scalability,  
465 thereby reducing uncertainties in projections such as gross primary productivity (127).  
466 Sequential coupling and Physics-Informed ML (PIML) further refine model accuracy by  
467 embedding ecological constraints within ML frameworks (31,128). Enriching observational  
468 datasets through open data sources, citizen science, and ML-driven remote sensing upscales  
469 point observations to continuous maps, enhancing model validation and calibration across  
470 diverse ecological contexts (129–131). Sustained funding is essential to maintain and expand  
471 these monitoring efforts, ensuring consistent long-term data collection and model  
472 advancement.

## 473 **6. Conclusions**

474 The hierarchical clustering and cluster map analyses offer a comprehensive understanding of  
475 the complexity and functionality of different ways to predict growth in different forest  
476 growth/vegetation models. By examining the connections between traits and model  
477 modalities, this study provides a description of the past and actual theories around the  
478 “growth” and a framework for selecting and developing models that are best suited to address  
479 specific forestry challenges, from local management practices to global ecological  
480 forecasting. This detailed analysis underscores the importance of aligning model complexity  
481 with the objectives of the research or management task at hand, ensuring that the chosen  
482 models provide accurate and actionable insights into forest growth and their dynamics.

483 This perspective underscores the need for a dynamic approach to forest growth modeling that  
484 embraces both theoretical and empirical dimensions. As we advance, the integration of  
485 diverse data sources and theoretical frameworks will be crucial in developing future models  
486 that are not only scientifically robust but also practically relevant in managing forests  
487 sustainably in a changing climate.

488

489 **Glossary**

490 ● *Forest growth model*: a computational tool used to simulate the dynamics of forest  
491 ecosystems over time, including changes in biomass, structure, and species  
492 composition. These models represent processes such as tree growth, mortality,  
493 regeneration, competition, and environmental conditions such as climate and nutrient  
494 availability.

495 ● *Photosynthetic-centric*: refers to approaches and methods that consider photosynthetic  
496 activity as the primary driver of the sink activity (tissue growth).

497 ● *Non-photosynthetic-centric*: refers to approaches and methods that consider growth as  
498 a result of a source-sink coordination, where tissue growth (sink) is regulated by both  
499 the availability of resources from photosynthesis (source) and environmental  
500 constraints.

501 ● *Spatial Scale*: refers to the spatial resolution at which the model operates, whether it is  
502 stand-specific, landscape-wide, or applicable to a terrestrial ecosystem scale.

503 ● *Temporal Resolution*: refers to the frequency processes representations within a  
504 model, ranging from daily to decadal time steps.

505 ● *Growth Processes*: approaches used to simulate growth, such as the allocation  
506 processes, photosynthesis models, and climate sensitivity (i.e. how growth responds to  
507 changing climate variables like temperature, precipitation, and atmospheric CO<sub>2</sub>  
508 levels)

509 ● *Mortality*: the process through which models simulate tree mortality, including stress-  
510 related and disturbance-related factors. This process, also if not strictly speaking  
511 refers to tree growth, controls community-level development and, therefore,

512 community growth. For more details on linking tree mortality to tree growth cf.  
513 Supplementary material, section 1.1.

514 • *Establishment*: the process that involves the probabilities that govern tree regeneration  
515 and establishment within the model. Similarly to the mortality process, the  
516 establishment process controls community-level development and, therefore, their  
517 growth. For more details on linking tree mortality to tree growth cf. Supplementary  
518 material, Section 1.1.

## 519 **Acknowledgements**

520 I.B. was supported by the project “SILVANUS - Integrated Technological and Information  
521 Platform for Wildfire Management” under grant agreement No. 101037247, which has  
522 received funding from the European Union’s Horizon 2020 Green Deal Research and  
523 Innovation Programme. D.D. and A.C. were supported by the European Union –  
524 NextGenerationEU under the National Recovery and Resilience Plan (NRRP), Mission 4  
525 Component 2 Investment 1.4 - Call for tender No. 3138 of December 16, 2021, rectified by  
526 Decree n.3175 of December 18, 2021 of the Italian Ministry of University and Research  
527 under award Number: Project code CN\_00000033, Concession Decree No. 1034 of June 17,  
528 2022 adopted by the Italian Ministry of University and Research, CUP B83C22002930006,  
529 Project title “National Biodiversity Future Centre - NBFC”

530

531

532

533

534

535

## 536 **References**

- 537 1. MA, editor. *Ecosystems and human well-being: synthesis*. Washington, DC: Island  
538 Press; 2005. 137 p.
- 539 2. Haines-Young R, Potschin M. *Common International Classification of Ecosystem  
540 Services (CICES, Version 4.1)*. 2013;
- 541 3. FAO. *Global Forest Resources Assessment 2020* [Internet]. FAO; 2020 [cited 2024 Aug  
542 28]. Available from: <http://www.fao.org/documents/card/en/c/ca8753en>
- 543 4. Brockerhoff EG, Barbaro L, Castagneyrol B, Forrester DI, Gardiner B, González-  
544 Olabarria JR, et al. Forest biodiversity, ecosystem functioning and the provision of  
545 ecosystem services. *Biodivers Conserv*. 2017 Dec 1;26(13):3005–35.
- 546 5. Senf C, Seidl R. Post-disturbance canopy recovery and the resilience of Europe's  
547 forests. *Glob Ecol Biogeogr*. 2022;31(1):25–36.
- 548 6. Keenan RJ. Climate change impacts and adaptation in forest management: a review.  
549 *Ann For Sci*. 2015 Mar;72(2):145–67.
- 550 7. Seidl R, Schelhaas MJ, Rammer W, Verkerk PJ. Increasing forest disturbances in  
551 Europe and their impact on carbon storage. *Nat Clim Change*. 2014 Sep;4(9):806–10.
- 552 8. Maréchaux I, Langerwisch F, Huth A, Bugmann H, Morin X, Reyer CPO, et al.  
553 Tackling unresolved questions in forest ecology: The past and future role of simulation  
554 models. *Ecol Evol*. 2021;11(9):3746–70.
- 555 9. Medlyn BE, Duursma RA, Zeppel MJB. Forest productivity under climate change: a  
556 checklist for evaluating model studies. *WIREs Clim Change*. 2011;2(3):332–55.
- 557 10. Reyer C. Forest Productivity Under Environmental Change—a Review of Stand-Scale  
558 Modeling Studies. *Curr For Rep*. 2015 Jun 1;1(2):53–68.
- 559 11. Blanco JA, Lo YH. Latest Trends in Modelling Forest Ecosystems: New Approaches or  
560 Just New Methods? *Curr For Rep*. 2023 Aug 1;9(4):219–29.
- 561 12. Seidl R, Thom D, Kautz M, Martín-Benito D, Peltoniemi M, Vacchiano G, et al. Forest  
562 disturbances under climate change. *Nat Clim Change*. 2017 Jul 1;7:395–402.
- 563 13. Hall A, Cox P, Huntingford C, Klein S. Progressing emergent constraints on future  
564 climate change. *Nat Clim Change*. 2019 Apr;9(4):269–78.
- 565 14. Raoult N, Jupp T, Booth B, Cox P. Combining local model calibration with the  
566 emergent constraint approach to reduce uncertainty in the tropical land carbon cycle  
567 feedback. *Earth Syst Dyn*. 2023 Jul 17;14(4):723–31.
- 568 15. Dakos V, Carpenter SR, Brock WA, Ellison AM, Guttal V, Ives AR, et al. Methods for  
569 Detecting Early Warnings of Critical Transitions in Time Series Illustrated Using  
570 Simulated Ecological Data. *PLOS ONE*. 2012 Jul 17;7(7):e41010.



- 571 16. Forzieri G, Dakos V, McDowell NG, Ramdane A, Cescatti A. Emerging signals of  
572 declining forest resilience under climate change. *Nature*. 2022 Aug;608(7923):534–9.
- 573 17. Guttal V, Jayaprakash C. Changing skewness: an early warning signal of regime shifts  
574 in ecosystems. *Ecol Lett*. 2008;11(5):450–60.
- 575 18. Keen RM, Voelker SL, Wang SYS, Bentz BJ, Goulden ML, Dangerfield CR, et al.  
576 Changes in tree drought sensitivity provided early warning signals to the California  
577 drought and forest mortality event. *Glob Change Biol*. 2022;28(3):1119–32.
- 578 19. Liu Y, Kumar M, Katul GG, Porporato A. Reduced resilience as an early warning signal  
579 of forest mortality. *Nat Clim Change*. 2019 Nov;9(11):880–5.
- 580 20. Vangi E, Dalmonech D, Cioccolo E, Marano G, Bianchini L, Puchi PF, et al. Stand age  
581 diversity (and more than climate change) affects forests’ resilience and stability,  
582 although unevenly. *J Environ Manage*. 2024 Aug 1;366:121822.
- 583 21. Dalmonech D, Marano G, Amthor JS, Cescatti A, Lindner M, Trotta C, et al. Feasibility  
584 of enhancing carbon sequestration and stock capacity in temperate and boreal European  
585 forests via changes to management regimes. *Agric For Meteorol*. 2022 Dec  
586 15;327:109203.
- 587 22. Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA. REVIEW: Searching for  
588 resilience: addressing the impacts of changing disturbance regimes on forest ecosystem  
589 services. *J Appl Ecol*. 2016;53(1):120–9.
- 590 23. Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, et al.  
591 Changing disturbance regimes, ecological memory, and forest resilience. *Front Ecol  
592 Environ*. 2016;14(7):369–78.
- 593 24. Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Venetier M, et al.  
594 A global overview of drought and heat-induced tree mortality reveals emerging climate  
595 change risks for forests. *For Ecol Manag*. 2010 Feb 5;259(4):660–84.
- 596 25. Díaz-Yáñez O, Käber Y, Anders T, Bohn F, Braziunas KH, Brūna J, et al. Tree  
597 regeneration in models of forest dynamics: A key priority for further research.  
598 *Ecosphere*. 2024;15(3):e4807.
- 599 26. Bugmann H, Seidl R, Hartig F, Bohn F, Brūna J, Cailleret M, et al. Tree mortality  
600 submodels drive simulated long-term forest dynamics: assessing 15 models from the  
601 stand to global scale. *Ecosphere*. 2019;10(2):e02616.
- 602 27. Mahnken M, Cailleret M, Collalti A, Trotta C, Biondo C, D’Andrea E, et al. Accuracy,  
603 realism and general applicability of European forest models. *Glob Change Biol*.  
604 2022;28(23):6921–43.
- 605 28. Friend AD, Lucht W, Rademacher TT, Keribin R, Betts R, Cadule P, et al. Carbon  
606 residence time dominates uncertainty in terrestrial vegetation responses to future climate  
607 and atmospheric CO<sub>2</sub>. *Proc Natl Acad Sci*. 2014 Mar 4;111(9):3280–5.

- 608 29. Prentice IC, Liang X, Medlyn BE, Wang YP. Reliable, robust and realistic: the three R's  
609 of next-generation land-surface modelling. *Atmospheric Chem Phys*. 2015 May  
610 29;15(10):5987–6005.
- 611 30. Fatichi S, Leuzinger S, Körner C. Moving beyond photosynthesis: from carbon source  
612 to sink-driven vegetation modeling. *New Phytol*. 2014;201(4):1086–95.
- 613 31. Raissi M, Perdikaris P, Karniadakis GE. Physics-informed neural networks: A deep  
614 learning framework for solving forward and inverse problems involving nonlinear  
615 partial differential equations. *J Comput Phys*. 2019 Feb 1;378:686–707.
- 616 32. McDowell NG, Fisher RA, Xu C, Domec JC, Hölttä T, Mackay DS, et al. Evaluating  
617 theories of drought-induced vegetation mortality using a multimodel–experiment  
618 framework. *New Phytol*. 2013;200(2):304–21.
- 619 33. Steinkamp J, Hickler T. Is drought-induced forest dieback globally increasing? *J Ecol*.  
620 2015;103(1):31–43.
- 621 34. De Kauwe MG, Sabot MEB, Medlyn BE, Pitman AJ, Meir P, Cernusak LA, et al.  
622 Towards species-level forecasts of drought-induced tree mortality risk. *New Phytol*.  
623 2022 Jul;235(1):94–110.
- 624 35. Schulze ED, Beck E, Buchmann N, Clemens S, Müller-Hohenstein K, Scherer-Lorenzen  
625 M. General Themes of Molecular Stress Physiology. In: Schulze ED, Beck E,  
626 Buchmann N, Clemens S, Müller-Hohenstein K, Scherer-Lorenzen M, editors. *Plant  
627 Ecology* [Internet]. Berlin, Heidelberg: Springer; 2019 [cited 2024 Nov 20]. p. 9–55.  
628 Available from: [https://doi.org/10.1007/978-3-662-56233-8\\_2](https://doi.org/10.1007/978-3-662-56233-8_2)
- 629 36. Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. Biomass allocation to  
630 leaves, stems and roots: meta-analyses of interspecific variation and environmental  
631 control. *New Phytol*. 2012;193(1):30–50.
- 632 37. Larcher W. *Physiological Plant Ecology: Ecophysiology and Stress Physiology of  
633 Functional Groups*. Springer Science & Business Media; 2003. 540 p.
- 634 38. Grime JP. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd  
635 Edition. 2nd edition. Chichester, West sussex ; New York, NY: Wiley; 2001. 456 p.
- 636 39. Hoch G, Richter A, Körner Ch. Non-structural carbon compounds in temperate forest  
637 trees. *Plant Cell Environ*. 2003;26(7):1067–81.
- 638 40. Landsberg J. Modelling forest ecosystems: state of the art, challenges, and future  
639 directions. *Can J For Res*. 2003 Mar;33(3):385–97.
- 640 41. Thornley JHM. A Balanced Quantitative Model for Root: Shoot Ratios in Vegetative  
641 Plants. *Ann Bot*. 1972 Mar;36(2):431–41.
- 642 42. Givnish TJ, editor. *On the Economy of Plant Form and Function: Proceedings of the  
643 Sixth Maria Moors Cabot Symposium*. Cambridge: Cambridge University Press; 1986.  
644 736 p.

- 645 43. Bloom AJ, F S Chapin III, Mooney HA. Resource Limitation in Plants-An Economic  
646 Analogy. *Annu Rev Ecol Evol Syst.* 1985 Nov 1;16(Volume 16,):363–92.
- 647 44. Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, et  
648 al. Vegetation demographics in Earth System Models: A review of progress and  
649 priorities. *Glob Change Biol.* 2018;24(1):35–54.
- 650 45. Fatichi S, Pappas C, Zscheischler J, Leuzinger S. Modelling carbon sources and sinks in  
651 terrestrial vegetation. *New Phytol.* 2019;221(2):652–68.
- 652 46. Gifford RM. Plant respiration in productivity models: conceptualisation, representation  
653 and issues for global terrestrial carbon-cycle research. *Funct Plant Biol.*  
654 2003;30(2):171–86.
- 655 47. Thornley JHM. Respiration, Growth and Maintenance in Plants. *Nature.* 1970  
656 Jul;227(5255):304–5.
- 657 48. Amthor JS. The McCree–de Wit–Penning de Vries–Thornley Respiration Paradigms: 30  
658 Years Later. *Ann Bot.* 2000 Jul 1;86(1):1–20.
- 659 49. Huang J, Hammerbacher A, Weinhold A, Reichelt M, Gleixner G, Behrendt T, et al.  
660 Eyes on the future – evidence for trade-offs between growth, storage and defense in  
661 Norway spruce. *New Phytol.* 2019;222(1):144–58.
- 662 50. Collalti A, Tjoelker MG, Hoch G, Mäkelä A, Guidolotti G, Heskell M, et al. Plant  
663 respiration: Controlled by photosynthesis or biomass? *Glob Change Biol.*  
664 2020;26(3):1739–53.
- 665 51. Landsberg JJ, Waring RH. A generalised model of forest productivity using simplified  
666 concepts of radiation-use efficiency, carbon balance and partitioning. *For Ecol Manag.*  
667 1997 Aug 1;95(3):209–28.
- 668 52. Collalti A, Perugini L, Santini M, Chiti T, Nolè A, Matteucci G, et al. A process-based  
669 model to simulate growth in forests with complex structure: Evaluation and use of 3D-  
670 CMCC Forest Ecosystem Model in a deciduous forest in Central Italy. *Ecol Model.*  
671 2014 Jan 24;272:362–78.
- 672 53. Collalti A, Marconi S, Ibrom A, Trotta C, Anav A, D’Andrea E, et al. Validation of 3D-  
673 CMCC Forest Ecosystem Model (v.5.1) against eddy covariance data for 10 European  
674 forest sites. *Geosci Model Dev.* 2016 Feb 8;9(2):479–504.
- 675 54. Nadal-Sala D, Sabaté S, Sánchez-Costa E, Poblador S, Sabater F, Gracia C. Growth and  
676 water use performance of four co-occurring riparian tree species in a Mediterranean  
677 riparian forest. *For Ecol Manag.* 2017 Jul 15;396:132–42.
- 678 55. Lasch-Born P, Suckow F, Reyer CPO, Gutsch M, Kollas C, Badeck FW, et al.  
679 Description and evaluation of the process-based forest model 4C v2.2 at four European  
680 forest sites. *Geosci Model Dev.* 2020 Nov 5;13(11):5311–43.
- 681 56. Scheller RM, Domingo JB, Sturtevant BR, Williams JS, Rudy A, Gustafson EJ, et al.  
682 Design, development, and application of LANDIS-II, a spatial landscape simulation  
683 model with flexible temporal and spatial resolution. *Ecol Model* 201 409419 [Internet].

- 684 2007 [cited 2024 Nov 20];201. Available from:  
685 <https://research.fs.usda.gov/treesearch/19237>
- 686 57. Seidl R, Rammer W, Scheller RM, Spies TA. An individual-based process model to  
687 simulate landscape-scale forest ecosystem dynamics. *Ecol Model.* 2012 Apr 24;231:87–  
688 100.
- 689 58. Smith B, Wårlind D, Arneth A, Hickler T, Leadley P, Siltberg J, et al. Implications of  
690 incorporating N cycling and N limitations on primary production in an individual-based  
691 dynamic vegetation model. *Biogeosciences.* 2014 Apr 10;11(7):2027–54.
- 692 59. Moreaux V, Martel S, Bosc A, Picart D, Achat D, Moisy C, et al. Energy, water and  
693 carbon exchanges in managed forest ecosystems: description, sensitivity analysis and  
694 evaluation of the INRAE GO+ model, version 3.0. *Geosci Model Dev.* 2020 Dec  
695 1;13(12):5973–6009.
- 696 60. Sato H, Itoh A, Kohyama T. SEIB–DGVM: A new Dynamic Global Vegetation Model  
697 using a spatially explicit individual-based approach. *Ecol Model.* 2007 Jan  
698 24;200(3):279–307.
- 699 61. Fisher RA, Muszala S, Verteinstein M, Lawrence P, Xu C, McDowell NG, et al. Taking  
700 off the training wheels: the properties of a dynamic vegetation model without climate  
701 envelopes, CLM4.5(ED). *Geosci Model Dev.* 2015 Nov 6;8(11):3593–619.
- 702 62. Friend AD, White A. Evaluation and analysis of a dynamic terrestrial ecosystem model  
703 under preindustrial conditions at the global scale. *Glob Biogeochem Cycles.*  
704 2000;14(4):1173–90.
- 705 63. Moorcroft PR, Hurtt GC, Pacala SW. A Method for Scaling Vegetation Dynamics: The  
706 Ecosystem Demography Model (ed). *Ecol Monogr.* 2001;71(4):557–86.
- 707 64. Scheiter S, Higgins SI. Impacts of climate change on the vegetation of Africa: an  
708 adaptive dynamic vegetation modelling approach. *Glob Change Biol.* 2009;15(9):2224–  
709 46.
- 710 65. Monteith JL, Moss CJ. Climate and the Efficiency of Crop Production in Britain [and  
711 Discussion]. *Philos Trans R Soc Lond B Biol Sci.* 1977;281(980):277–94.
- 712 66. Farquhar GD, von Caemmerer S, Berry JA. A biochemical model of photosynthetic  
713 CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta.* 1980 Jun 1;149(1):78–90.
- 714 67. De Pury DGG, Farquhar GD. Simple scaling of photosynthesis from leaves to canopies  
715 without the errors of big-leaf models. *Plant Cell Environ.* 1997;20(5):537–57.
- 716 68. Körner C. Paradigm shift in plant growth control. *Curr Opin Plant Biol.* 2015  
717 Jun;25:107–14.
- 718 69. Vuichard N, Messina P, Luyssaert S, Guenet B, Zaehle S, Ghattas J, et al. Accounting  
719 for carbon and nitrogen interactions in the global terrestrial ecosystem model  
720 ORCHIDEE (trunk version, rev 4999): multi-scale evaluation of gross primary  
721 production. *Geosci Model Dev.* 2019 Nov 20;12(11):4751–79.

- 722 70. Zeng J, Li X, Song R, Xie H, Li X, Liu W, et al. Mechanisms of litter input changes on  
723 soil organic carbon dynamics: a microbial carbon use efficiency-based perspective. *Sci*  
724 *Total Environ.* 2024 Nov 1;949:175092.
- 725 71. Ma B, Wang Y, Ge J, Xie Z. Patterns and controls of leaf litter nitrogen and phosphorus  
726 of broad-leaved tree species across and within the tropics and the extra-tropics. *Agric*  
727 *For Meteorol.* 2024 Nov 15;358:110249.
- 728 72. Bunn RA, Corrêa A, Joshi J, Kaiser C, Lekberg Y, Prescott CE, et al. What determines  
729 transfer of carbon from plants to mycorrhizal fungi? *New Phytol.* 2024;244(4):1199–  
730 215.
- 731 73. Dewar RC, Franklin O, Mäkelä A, McMurtrie RE, Valentine HT. Optimal Function  
732 Explains Forest Responses to Global Change. *BioScience.* 2009 Feb 1;59(2):127–39.
- 733 74. Gessler A, Zweifel R. Beyond source and sink control – toward an integrated approach  
734 to understand the carbon balance in plants. *New Phytol.* 2024;242(3):858–69.
- 735 75. Brodribb TJ, Skelton RP, McAdam SAM, Bienaimé D, Lucani CJ, Marmottant P.  
736 Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *New*  
737 *Phytol.* 2016;209(4):1403–9.
- 738 76. Katul G, Manzoni S, Palmroth S, Oren R. A stomatal optimization theory to describe the  
739 effects of atmospheric CO<sub>2</sub> on leaf photosynthesis and transpiration. *Ann Bot.* 2010  
740 Mar 1;105(3):431–42.
- 741 77. Trugman AT. Integrating plant physiology and community ecology across scales  
742 through trait-based models to predict drought mortality. *New Phytol.* 2022;234(1):21–7.
- 743 78. Sabot MEB, De Kauwe MG, Pitman AJ, Medlyn BE, Verhoef A, Ukkola AM, et al.  
744 Plant profit maximization improves predictions of European forest responses to drought.  
745 *New Phytol.* 2020 Jun;226(6):1638–55.
- 746 79. Wutzler T, Zaehle S, Schrumppf M, Ahrens B, Reichstein M. Adaptation of microbial  
747 resource allocation affects modelled long term soil organic matter and nutrient cycling.  
748 *Soil Biol Biochem.* 2017 Dec 1;115:322–36.
- 749 80. Barbaroux C, Bréda N. Contrasting distribution and seasonal dynamics of carbohydrate  
750 reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees.  
751 *Tree Physiol.* 2002 Dec 1;22(17):1201–10.
- 752 81. Fischer R, Bohn F, Dantas de Paula M, Dislich C, Groeneveld J, Gutiérrez AG, et al.  
753 Lessons learned from applying a forest gap model to understand ecosystem and carbon  
754 dynamics of complex tropical forests. *Ecol Model.* 2016 Apr 24;326:124–33.
- 755 82. Bugmann H, Fischlin A, Kienast F. Model convergence and state variable update in  
756 forest gap models. *Ecol Model.* 1996 Aug 1;89(1):197–208.
- 757 83. ABER JD, OLLINGER SV, DRISCOLL CT, FEDERER CA, REICH PB. PnET  
758 Models: Carbon, Nitrogen, Water Dynamics in Forest Ecosystems (Vers. 4 and 5)  
759 [Internet]. ORNL Distributed Active Archive Center; 2005 [cited 2024 Nov 21]. p.  
760 2.4576 MB. Available from: [http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds\\_id=817](http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=817)

- 761 84. Dufrière E, Davi H, François C, Maire G le, Dantec VL, Granier A. Modelling carbon  
762 and water cycles in a beech forest: Part I: Model description and uncertainty analysis on  
763 modelled NEE. *Ecol Model.* 2005 Jul 10;185(2):407–36.
- 764 85. Williams M, Rastetter EB, Fernandes DN, Goulden ML, Wofsy SC, Shaver GR, et al.  
765 Modelling the soil-plant-atmosphere continuum in a *Quercus*–*Acer* stand at Harvard  
766 Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic  
767 properties. *Plant Cell Environ.* 1996;19(8):911–27.
- 768 86. Grünig M, Rammer W, Albrich K, André F, Augustynczyk ALD, Bohn F, et al. A  
769 harmonized database of European forest simulations under climate change. *Data Brief.*  
770 2024 Jun 1;54:110384.
- 771 87. Dalmonech D, Vangi E, Chiesi M, Chirici G, Fibbi L, Giannetti F, et al. Regional  
772 estimates of gross primary production applying the Process-Based Model 3D-CMCC-  
773 FEM vs. Remote-Sensing multiple datasets. *Eur J Remote Sens.* 2024 Dec  
774 31;57(1):2301657.
- 775 88. Minunno F, Peltoniemi M, Härkönen S, Kalliokoski T, Makinen H, Mäkelä A. Bayesian  
776 calibration of a carbon balance model PREBAS using data from permanent growth  
777 experiments and national forest inventory. *For Ecol Manag.* 2019 May 15;440:208–57.
- 778 89. Gutsch M, Lasch-Born P, Suckow F, Reyer CPO. Evaluating the productivity of four  
779 main tree species in Germany under climate change with static reduced models. *Ann For  
780 Sci.* 2016 Jun;73(2):401–10.
- 781 90. Schumacher S, Bugmann H, Mladenoff DJ. Improving the formulation of tree growth  
782 and succession in a spatially explicit landscape model. *Ecol Model.* 2004 Dec  
783 10;180(1):175–94.
- 784 91. Thrippleton T, Dolos K, Perry GLW, Groeneveld J, Reineking B. Simulating long-term  
785 vegetation dynamics using a forest landscape model: the post-Taupo succession on Mt  
786 Hauhungatahi, North Island, New Zealand. *N Z J Ecol.* 2014;38(1):26–38.
- 787 92. Keane RE, Ryan KC, Running SW. Simulating effects of fire on northern Rocky  
788 Mountain landscapes with the ecological process model FIRE-BGC. *Tree Physiol.* 1996  
789 Mar 1;16(3):319–31.
- 790 93. Wehrli A, Weisberg PJ, Schönenberger W, Brang P, Bugmann H. Improving the  
791 establishment submodel of a forest patch model to assess the long-term protective effect  
792 of mountain forests. *Eur J For Res.* 2007 Jan 1;126(1):131–45.
- 793 94. Lawrence DM, Fisher RA, Koven CD, Oleson KW, Swenson SC, Bonan G, et al. The  
794 Community Land Model Version 5: Description of New Features, Benchmarking, and  
795 Impact of Forcing Uncertainty. *J Adv Model Earth Syst.* 2019;11(12):4245–87.
- 796 95. Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, et al. A  
797 dynamic global vegetation model for studies of the coupled atmosphere-biosphere  
798 system. *Glob Biogeochem Cycles* [Internet]. 2005 [cited 2024 Nov 21];19(1). Available  
799 from: <https://onlinelibrary.wiley.com/doi/abs/10.1029/2003GB002199>

- 800 96. Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, et al. Evaluation of  
801 ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic  
802 global vegetation model. *Glob Change Biol.* 2003;9(2):161–85.
- 803 97. Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, et al. An integrated  
804 biosphere model of land surface processes, terrestrial carbon balance, and vegetation  
805 dynamics. *Glob Biogeochem Cycles.* 1996;10(4):603–28.
- 806 98. O’ishi R, Abe-Ouchi A. Influence of dynamic vegetation on climate change arising from  
807 increasing CO<sub>2</sub>. *Clim Dyn.* 2009 Oct 1;33(5):645–63.
- 808 99. Merganičová K, Merganič J, Lehtonen A, Vacchiano G, Sever MZO, Augustynczik  
809 ALD, et al. Forest carbon allocation modelling under climate change. *Tree Physiol.*  
810 2019 Dec 1;39(12):1937–60.
- 811 100. Medlyn BE, Dreyer E, Ellsworth D, Forstreuter M, Harley PC, Kirschbaum MUF, et al.  
812 Temperature response of parameters of a biochemically based model of photosynthesis.  
813 II. A review of experimental data. *Plant Cell Environ.* 2002;25(9):1167–79.
- 814 101. Haxeltine A, Prentice IC. BIOME3: An equilibrium terrestrial biosphere model based on  
815 ecophysiological constraints, resource availability, and competition among plant  
816 functional types. *Glob Biogeochem Cycles.* 1996;10(4):693–709.
- 817 102. Monteith JL. Solar Radiation and Productivity in Tropical Ecosystems. *J Appl Ecol.*  
818 1972;9(3):747–66.
- 819 103. Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H. A  
820 Continuous Satellite-Derived Measure of Global Terrestrial Primary Production.  
821 *BioScience.* 2004 Jun 1;54(6):547–60.
- 822 104. Waring RH, Landsberg JJ, Williams M. Net primary production of forests: a constant  
823 fraction of gross primary production? *Tree Physiol.* 1998 Feb 1;18(2):129–34.
- 824 105. Van Oijen M, Rougier J, Smith R. Bayesian calibration of process-based forest models:  
825 bridging the gap between models and data. *Tree Physiol.* 2005 Jul 1;25(7):915–27.
- 826 106. Collalti A, Prentice IC. Is NPP proportional to GPP? Waring’s hypothesis 20 years on.  
827 *Tree Physiol.* 2019 Aug 1;39(8):1473–83.
- 828 107. Collalti A, Ibrom A, Stockmarr A, Cescatti A, Alkama R, Fernández-Martínez M, et al.  
829 Forest production efficiency increases with growth temperature. *Nat Commun.* 2020 Oct  
830 21;11(1):5322.
- 831 108. de Wergifosse `Louis, André F, Goosse H, Boczon A, Cecchini S, Ciceu A, et al.  
832 Simulating tree growth response to climate change in structurally diverse oak and beech  
833 forests. *Sci Total Environ.* 2022 Feb 1;806:150422.
- 834 109. He HS. Forest landscape models: Definitions, characterization, and classification. *For*  
835 *Ecol Manag.* 2008 Feb 10;254(3):484–98.

- 836 110. Fontes L, Bontemps JD, Bugmann H, Van Oijen M, Gracia C, Kramer K, et al. Models  
837 for supporting forest management in a changing environment. *For Syst.* 2011 Jan  
838 12;3(4):8.
- 839 111. Zhang-Zheng H, Deng X, Aguirre-Gutiérrez J, Stocker BD, Thomson E, Ding R, et al.  
840 Why models underestimate West African tropical forest primary productivity. *Nat*  
841 *Commun.* 2024 Nov 6;15(1):9574.
- 842 112. Dunkl I, Lovenduski N, Collalti A, Arora VK, Ilyina T, Brovkin V. Gross primary  
843 productivity and the predictability of CO<sub>2</sub>: more uncertainty in what we predict than  
844 how well we predict it. *Biogeosciences.* 2023 Aug 23;20(16):3523–38.
- 845 113. Hegerl GC, Ballinger AP, Booth BBB, Borchert LF, Brunner L, Donat MG, et al.  
846 Toward Consistent Observational Constraints in Climate Predictions and Projections.  
847 *Front Clim [Internet].* 2021 Jun 9 [cited 2024 Nov 21];3. Available from:  
848 <https://www.frontiersin.org/journals/climate/articles/10.3389/fclim.2021.678109/full>
- 849 114. Hamant O. Debunking the idea of biological optimisation: quantitative biology to the  
850 rescue. *Quant Plant Biol.* 2024;5:e3.
- 851 115. Anten NPR. Optimal Photosynthetic Characteristics of Individual Plants in Vegetation  
852 Stands and Implications for Species Coexistence. *Ann Bot.* 2004 Dec 13;95(3):495–506.
- 853 116. Bull JJ, Wang IN. REVIEW: Optimality models in the age of experimental evolution  
854 and genomics. *J Evol Biol.* 2010;23(9):1820–38.
- 855 117. Mäkelä A, Givnish T, Berninger F, Buckley T, Farquhar G, Hari P. Challenges and  
856 opportunities of the optimality approach in plant ecology. *Silva Fenn [Internet].* 2002  
857 [cited 2024 Nov 21];36(3). Available from: <https://www.silvafennica.fi/article/528>
- 858 118. Zaehle S, Dalmonech D. Carbon–nitrogen interactions on land at global scales: current  
859 understanding in modelling climate biosphere feedbacks. *Curr Opin Environ Sustain.*  
860 2011 Oct 1;3(5):311–20.
- 861 119. Fisher JB, Sitch S, Malhi Y, Fisher RA, Huntingford C, Tan SY. Carbon cost of plant  
862 nitrogen acquisition: A mechanistic, globally applicable model of plant nitrogen uptake,  
863 retranslocation, and fixation. *Glob Biogeochem Cycles [Internet].* 2010 [cited 2024 Nov  
864 21];24(1). Available from:  
865 <https://onlinelibrary.wiley.com/doi/abs/10.1029/2009GB003621>
- 866 120. Franklin JF, Spies TA, Pelt RV, Carey AB, Thornburgh DA, Berg DR, et al.  
867 Disturbances and structural development of natural forest ecosystems with silvicultural  
868 implications, using Douglas-fir forests as an example. *For Ecol Manag.* 2002 Jan  
869 1;155(1):399–423.
- 870 121. Dewar R, Mauranen A, Mäkelä A, Hölttä T, Medlyn B, Vesala T. New insights into the  
871 covariation of stomatal, mesophyll and hydraulic conductances from optimization  
872 models incorporating nonstomatal limitations to photosynthesis. *New Phytol.*  
873 2018;217(2):571–85.
- 874 122. Zaehle S, Sitch S, Smith B, Hatterman F. Effects of parameter uncertainties on the  
875 modeling of terrestrial biosphere dynamics. *Glob Biogeochem Cycles [Internet].* 2005



- 876 [cited 2023 Feb 15];19(3). Available from:  
877 <https://onlinelibrary.wiley.com/doi/abs/10.1029/2004GB002395>
- 878 123. Bugmann H, Seidl R. The evolution, complexity and diversity of models of long-term  
879 forest dynamics. *J Ecol.* 2022;110(10):2288–307.
- 880 124. Raissi M. Deep Hidden Physics Models: Deep Learning of Nonlinear Partial  
881 Differential Equations [Internet]. arXiv; 2018 [cited 2024 Aug 28]. Available from:  
882 <http://arxiv.org/abs/1801.06637>
- 883 125. Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ. TreeMig: A forest-  
884 landscape model for simulating spatio-temporal patterns from stand to landscape scale.  
885 *Ecol Model.* 2006 Dec 16;199(4):409–20.
- 886 126. Yu Q, Tolson BA, Shen H, Han M, Mai J, Lin J. Enhancing long short-term memory  
887 (LSTM)-based streamflow prediction with a spatially distributed approach. *Hydrol  
888 Earth Syst Sci.* 2024 May 14;28(9):2107–22.
- 889 127. Schlund M, Eyring V, Camps-Valls G, Friedlingstein P, Gentine P, Reichstein M.  
890 Constraining Uncertainty in Projected Gross Primary Production With Machine  
891 Learning. *J Geophys Res Biogeosciences.* 2020;125(11):e2019JG005619.
- 892 128. Yu X, Zhong L, Zhou H, Gong L, Wei L. Tree-Ring Based Forest Model Calibrations  
893 with a Deep Learning Algorithm [Internet]. Rochester, NY; 2024 [cited 2024 Feb 19].  
894 Available from: <https://papers.ssrn.com/abstract=4681130>
- 895 129. Vangi E, D’Amico G, Francini S, Borghi C, Giannetti F, Corona P, et al. Large-scale  
896 high-resolution yearly modeling of forest growing stock volume and above-ground  
897 carbon pool. *Environ Model Softw.* 2023 Jan 1;159:105580.
- 898 130. Bodesheim P, Babst F, Frank DC, Hartl C, Zang CS, Jung M, et al. Predicting  
899 spatiotemporal variability in radial tree growth at the continental scale with machine  
900 learning. *Environ Data Sci.* 2022 Jan 1;1:e9.
- 901 131. Qiu R, Han G, Ma X, Xu H, Shi T, Zhang M. A Comparison of OCO-2 SIF, MODIS  
902 GPP, and GOSIF Data from Gross Primary Production (GPP) Estimation and Seasonal  
903 Cycles in North America. *Remote Sens.* 2020 Jan;12(2):258.
- 904 132. Weng E, Aleinov I, Singh R, Puma MJ, McDermid SS, Kiang NY, et al. Modeling  
905 demographic-driven vegetation dynamics and ecosystem biogeochemical cycling in  
906 NASA GISS’s Earth system model (ModelE-BiomeE v.1.0). *Geosci Model Dev.* 2022  
907 Nov 14;15(22):8153–80.
- 908 133. Buotte PC, Koven CD, Xu C, Shuman JK, Goulden ML, Levis S, et al. Capturing  
909 functional strategies and compositional dynamics in vegetation demographic models.  
910 *Biogeosciences.* 2021 Jul 30;18(14):4473–90.
- 911 134. Bugmann H. On the ecology of mountainous forests in a changing climate: a simulation  
912 study [Internet] [Doctoral Thesis]. ETH Zürich; 1994 [cited 2024 Nov 21]. Available  
913 from: <https://www.research-collection.ethz.ch/handle/20.500.11850/141625>

- 914 135. Scheller RM, Mladenoff DJ. A forest growth and biomass module for a landscape  
915 simulation model, LANDIS: design, validation, and application. *Ecol Model.* 2004 Dec  
916 10;180(1):211–29.
- 917 136. Pacala SW, Deutschman DH. Details That Matter: The Spatial Distribution of Individual  
918 Trees Maintains Forest Ecosystem Function. *Oikos.* 1995;74(3):357–65.
- 919 137. Hanbury-Brown AR, Ward RE, Kueppers LM. Forest regeneration within Earth system  
920 models: current process representations and ways forward. *New Phytol.*  
921 2022;235(1):20–40.
- 922

923 **Tables**

924 **Table 1:** *Overview of forest growth model traits. Each trait is linked to specific components*  
 925 *and subcomponents that describe how the models approach different ecological processes.*

<b>Trait</b>	<b>component</b>	<b>sub-components</b>
model structure	approach to model productivity and growth	optimum equation, NPP
model structure	allocation	dynamic coefficients, carbon balance, none
model structure	climate-sensitivity	temperature, CO <sub>2</sub> , WUE, phenology, soil moisture
temporal resolution	time-step to model productivity	daily, monthly, annual
temporal resolution	time-step for environmental influence	daily, monthly, annual
spatial resolution	scale	stand, landscape, global

926 **Table 2:** Categorization of Forest Growth Models Based on Traits and Modality Complexity. Each trait is identified by a specific code and  
 927 prefix, linked to either the whole modeling system, spatial resolution, or growth. The categories include modeling approaches, species-specific  
 928 dynamics, and time-step intervals for productivity and environmental influences.

929

Category	Trait name	Code	Prefix	Category	Identifier
0) Whole modelling system (after Merganičová et al. 2019)	Modelling approach	<i>MS_A</i>	Modelling system (MS)	-	Approach (A)
	Dominant modelling concept	<i>MS_C</i>	Modelling system (MS)	-	Concept (C)
	Dynamics are species- or PFT-specific?	<i>MS_SPF_T</i>	Modelling system (MS)	-	Species or PFT-specific (SPFT)
1) Spatial resolution	Spatial Scale	<i>SC_SP</i>	Scale (SC)	-	Spatial Scale (SC)
	Forest species composition	<i>SC_SC</i>	Scale (SC)	-	Species composition (SC)
	Forest vertical stratification	<i>SC_VS</i>	Scale (SC)	-	Vertical stratification (VS)
	Forest horizontal structure	<i>SC_HS</i>	Scale (SC)	-	Horizontal structure (HS)
	Forest age composition	<i>SC_AC</i>	Scale (SC)	-	Age composition (AC)
2) Growth	Time step for update of tree geometry	<i>GR_TSU_TG</i>	Growth (GR)	Time Step (TSU)	Tree geometry (TG)
	Time step for modeling of tree productivity	<i>GR_TSU_TP</i>	Growth (GR)	Time Step (TSU)	Tree productivity (TP)
	Time step for environmental influences	<i>GR_TSU_EI</i>	Growth (GR)	Time Step (TSU)	Environmental Influence (EI)

	Photosynthesis modeling approach	GR_PM A	Growth (GR)	-	Photosynthesis modeling approach (PMA)
	Autotrophic respiration	GR_AR	Growth (GR)	-	Autotrophic Respiration (AR)
	Allocation	GR_A	Growth (GR)	-	Allocation (A)
	Allocation processes	GR_AP	Growth (GR)	-	Allocation Processes (AP)
	Structural / Non-structural Carbon	GR_SN SC	Growth (GR)	-	Structural / Non-structural Carbon SNSC (SNSC)
	Photosynthesis model	<i>GR_PM</i>	Growth (GR)	-	Photosynthesis model (PM)
	Temperature	GR_T	Growth (GR)	-	Temperature (T)
	Soil moisture	GR_SM	Growth (GR)	-	Soil Moisture (SM)
	Nutrients	GR_N	Growth (GR)	-	Nutrients (N)
	CO <sub>2</sub>	GR_CO <sub>2</sub>	Growth (GR)	-	Ca concentration (CO <sub>2</sub> )
	WUE	GR_WU E	Growth (GR)	-	Water use efficiency (WUE)
	Phenology	GR_P	Growth (GR)	-	Phenology (P)
3) Mortality	Background mortality	MO_BM	Mortality (MO)	-	Background Mortality (BM)
	Stress-related mortality	MO_SM	Mortality (MO)	-	Stress Mortality (SM)
	Disturbance mortality	MO_D M	Mortality (MO)	-	Disturbance Mortality (DM)

4) Establishment	Modeling approach	ES_A	Establishment (ES)	-	Approach (A)
	Probability	ES_P	Establishment (ES)	-	Probability (P)
	Ingrowth threshold	ES_IT	Establishment (ES)	-	Ingrowth threshold (IT)
	Browsing	ES_B	Establishment (ES)	-	Browsing (B)
	Seed production	ES_SP	Establishment (ES)	-	Seed Production (SP)
	Dispersal	ES_D	Establishment (ES)	-	Dispersal (D)

930

931

932

933

934

935

936

937

938

939 **Table 3:** *Modality Complexity in Forest Growth Models, ranging from hybrid to mechanistic and empirical approaches. Our analysis covers traits*  
940 *related to species-specific dynamics, spatial scales (globe, landscape, stand), forest structure (monoculture, multispecies), temporal resolution*  
941 *(decadal to sub-daily), and the modeling approach (photosynthetic-centric vs. non-photosynthetic-centric). The table highlights how each trait's*  
942 *complexity increases across modalities, providing insights into the trade-offs between model accuracy and computational demand.*

Modality (complexity)					
MOD1	MOD2	MOD3	MOD4	MOD5	MOD6
Hybrid (1)	Mechanistic (2)				
Empirical (1)	Process-based (2)				
PFT-specific (1)	Species-specific (2)				
Globe (1)	Landscape (2)	Stand (3)			
Monoculture (1)	Multispecies (2)				
Monolayer (1)	Multilayer (2)				
spatially implicit (1)	spatially explicit (2)				
Even-Aged (1)	Uneven-Aged (2)				
Decadal (1)	Annual (2)	Monthly (3)	Daily (4)		
Decadal (1)	Annual (2)	Monthly (3)	Daily (4)	Sub-daily (5)	
Decadal (1)	Annual (2)	Monthly (3)	Daily (4)	Sub-daily (5)	
Non-Photosynthetic-centric (1)	Photosynthetic-centric (2)				
NA (no carbon balance) (0)	Fixed coefficients (1)	GMRP (2)			
NA (no carbon balance) (0)	Fixed coefficients (1)	Fixed coefficients (via allocation) (2)	Dynamic coefficients (3)		
Fixed ratios (1)	Allometry and resource limitation (2)	Root-shoot functional	Pipe model (4)	Source-sink model (5)	

		balance (3)			
No (0)	Yes (1)				
Empirical (response curve) (1)	Empirical (LUE) (2)	Semi-Empirical (Haxeltine & Prentice) (3)	Mechanistic (Farquhar) (4)		
Response curve (e.g. to DD) (1)	Mechanistic (T-dependency of PS, R, ...) (2)				
Semi-Empirical (Response curve (e.g. to SM or DrIndex)) (1)	Stomatal conductance (2)	Mechanistic (3)			
No (0)	Empirical (Response curve) (1)	Mechanistic (from soil model/module) (2)			
No (0)	Empirical (Response curve) (1)	Ci/Ca (2)			
No (0)	Response curve (1)	Coupled photosynthesis-stomatal conductance (2)			
T-controlled (1)	Eliophany (1)	VPD (1)	Resource limitation (2)	Parallel model (2)	Alternate model (2)
No (0)	Constant (1)	Increasing with age (2)	Increasing with size (2)	Increasing with age and size (2)	Decreasing with photosynthesis efficiency (3)
No (0)	Threshold approach (1)	Increment-related (2)	Productivity-related (2)	Reserves depletion (Carbon starvation) (3)	
No (0)	Yes (1)				
User defined recruitment (1)	Bernoulli (2)	Poisson (2)	Hurdle (2)		



No (0)	Random (1)	Rate (1)	Random, modified by environment (2)		
No (0)	0 < dbh < 2 cm (1)	Age class (1)	h < 50 cm (1)	50 < h < 130 cm (1)	
No (0)	Static (1)	Dynamic (2)			
No (0)	Simple model (no masting) (1)	Complex model (w/ masting) (2)			
No (0)	Single exponential kernel (1)	Double exponential kernel (1)			

943

944

945

946

947

948

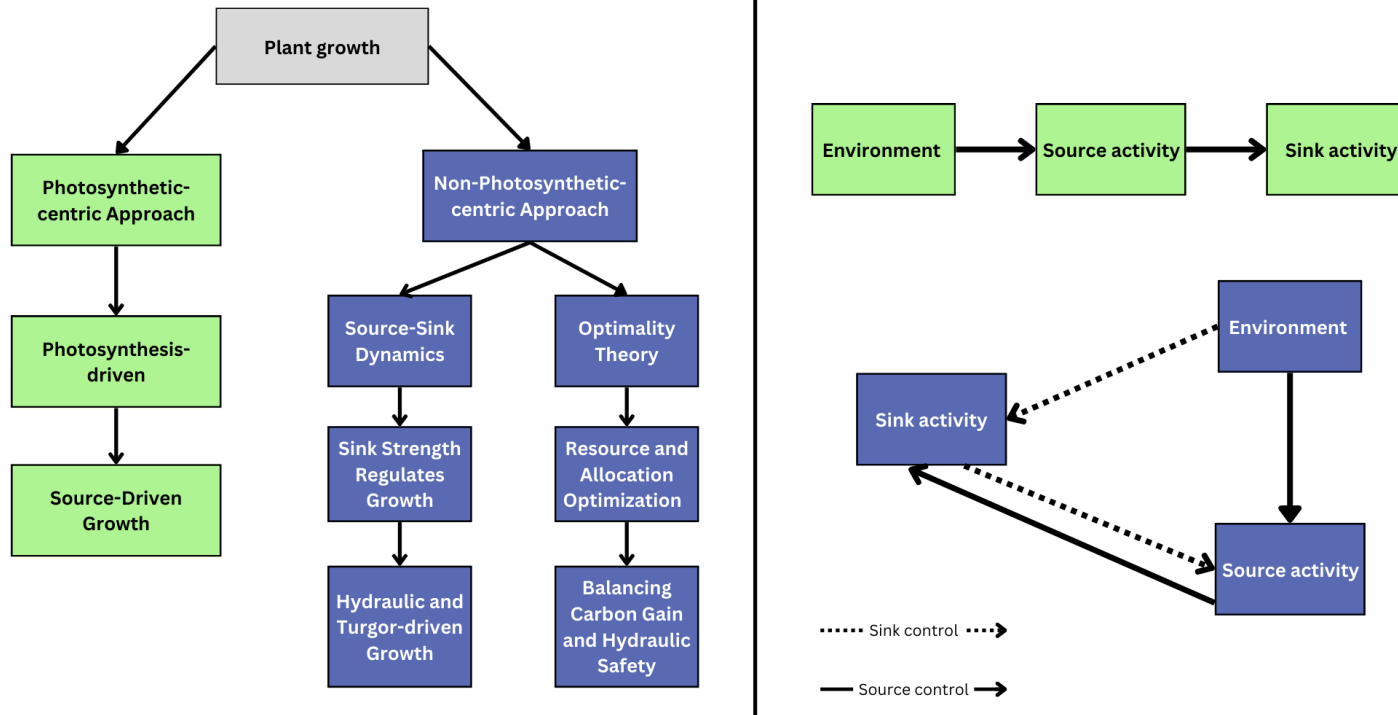
949

950

951

952

953 **Figures**



954

955 **Figure 1:** Conceptual representation of plant growth modeling approaches, modified after Körner (68). (a) The left panel outlines the  
 956 photosynthesis theories and their representation. (b) The right panel shows the interaction between "Environment," "Source Activity," and "Sink  
 957 Activity," showing a linear flow for the Photosynthetic-centric approach (in green) and feedback loops for the Non-Photosynthetic-centric  
 958 approach (in blue), with solid arrows for source control and dashed arrows for sink control.



### Enhancing Process Representation

- Legacy effect and optimality theory integration
- ML- driven modular coupling
- Dynamic and real-time feedback from ML models



### Calibrating parameters with constraints

- Real-time adaptive calibration using ML
- Multi-objective optimization for trade-offs
- Physics-informed ML (PIML) for constraints
- Sequential coupling to reduce residuals and capture anomalies

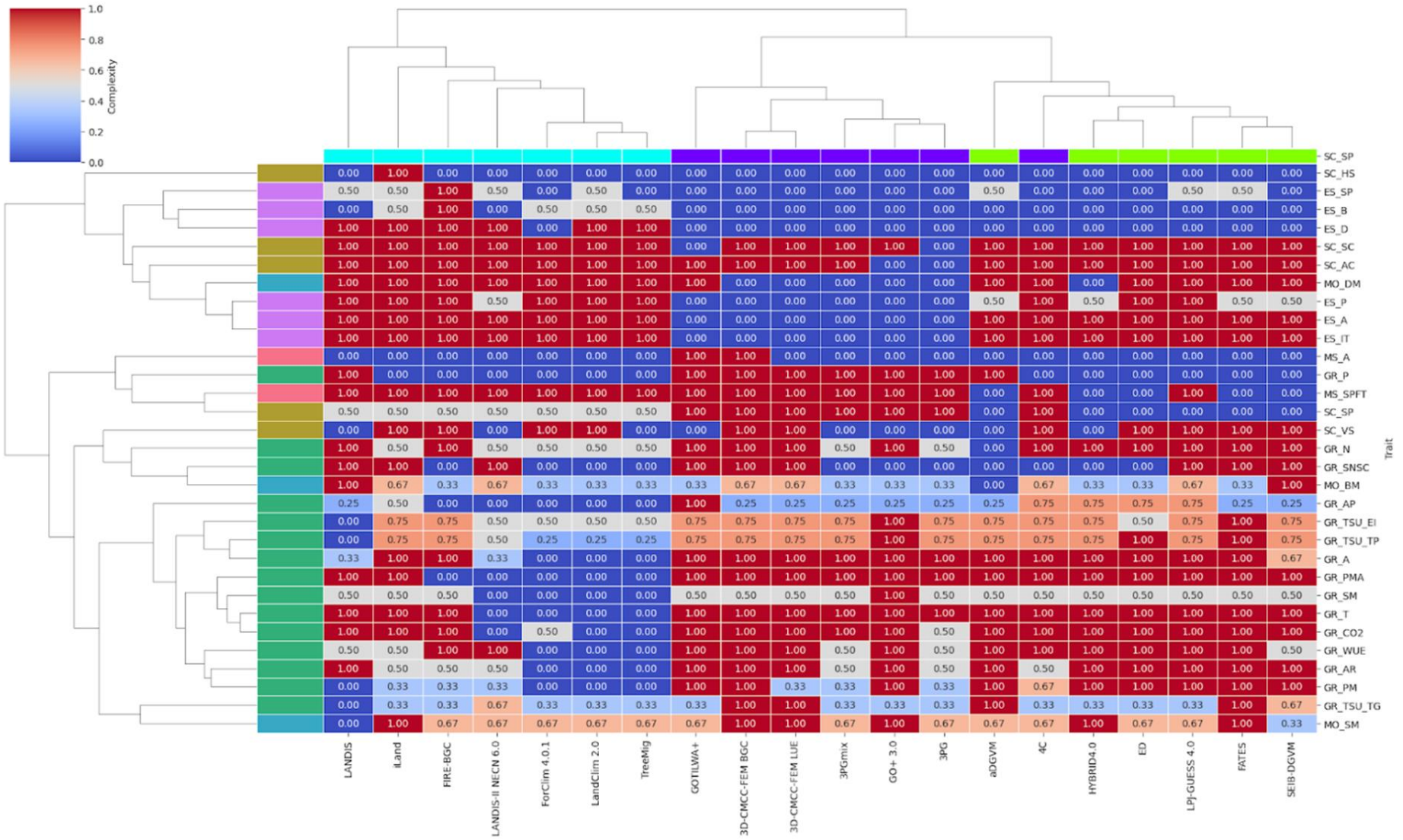
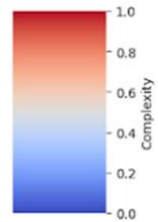


### Enhancing Observation Datasets

- Extensive open data sources (LTER, ICP, ICOS)
- Crowdsourced data and citizen science
- ML upscaling via remote sensing

959

960 **Figure 2:** Proposed framework for enhancing forest growth modeling



962 **Figure 3:** Hierarchical clustering of 18 process-based forest growth models based on modality complexity. The clustermap illustrates the relative  
963 complexity of different traits across the models, with color intensity representing the level of complexity (darker shades indicate higher  
964 complexity). The models are grouped into three primary clusters: (1) Low complexity models, which primarily operate at the stand scale with  
965 simpler structural components; (2) Moderate complexity models, which function at the landscape scale, incorporating more detailed spatial and  
966 temporal processes; and (3) High complexity models, which operate at the global scale and integrate a wide range of dynamic environmental  
967 interactions and sophisticated allocation processes. Key traits analyzed include spatial and temporal resolution, mortality processes, carbon  
968 allocation, and climate sensitivity. This clustering helps to categorize models based on their suitability for different research and management  
969 objectives, ranging from local stand management to global climate change forecasting.

970

971

972

973

974

975

976

977

## Supplementary materials

978

# Modeling forest growth under climate change

979

Boukhris et al., 2024

980

### 1.1 Regeneration and Tree mortality

981

At a relatively coarse spatial scale (e.g., stand and landscape), the net growth concept is used,

982

which considers not only the growth of e.g. single pools or individual trees but also includes

983

mortality (tree death) and recruitment. Mortality and regeneration are integral to forest

984

growth modeling since these processes because their dynamics help simulate the full

985

dynamics of forest ecosystems and tree communities, directly has a direct influence on

986

influencing their growth and the overall forest structure (132,133). Accurately modeling tree

987

growth (Section 2), has instead direct and direct implications on implication to growth

988

dynamics, for instance the process of recruitment (via the allocation of resources to seeds

989

rather than woody structure) and mortality via (e.g. self-thinning or carbon starvation).

990

Including all these processes ensures that models can capture the cyclical nature of forests,

991

where growth is constantly balanced by tree death (mortality) and new tree establishment

992

(regeneration). Here's why they are closely tied to growth modeling:

993

#### - Mortality as a Growth Regulator:

994

Mortality is not a separate process but a direct counterbalance to growth. As trees grow,

995

competition for resources like light, water, and nutrients increases, leading to stress-related or

996

disturbance-induced mortality. In growth models like ForClim (134), LANDIS-II (135), and

997

SORTIE (136), mortality is explicitly linked to growth conditions. If growth rates are high,

998

competition may lead to higher mortality as trees compete for limited resources. Conversely,

999 low-growth conditions (e.g., drought or nutrient limitations) often result in increased  
1000 mortality to reflect the decreased ability of trees to maintain themselves under stress.

1001 - Regeneration and Growth Potential:

1002 Regeneration is essential for maintaining forest growth over time. Without the establishment  
1003 of new trees, forests would eventually decline as older trees die. Regeneration processes, such  
1004 as seedling establishment and sapling growth, directly influence forest composition and the  
1005 potential for future growth. Models like SORTIE (136) and LPJ-GUESS (58) incorporate  
1006 detailed regeneration rules that depend on environmental factors like light availability,  
1007 competition, and disturbance regimes. These processes determine the species that will  
1008 dominate the forest in the future, shaping long-term growth patterns.

1009 - Growth-Mortality-Regeneration Feedback Loops:

1010 Growth models use mortality and regeneration to create feedback loops that regulate forest  
1011 structure. For instance, high growth rates in early forest development phases can be followed  
1012 by increased mortality due to self-thinning, where trees die off as competition intensifies.  
1013 Regeneration also plays a critical role in these loops, as gaps created by mortality allow for  
1014 new seedlings to establish, fostering a new cycle of growth. Without integrating these  
1015 processes, growth models would overestimate forest biomass accumulation and fail to  
1016 represent realistically the ecosystem dynamics (137).

1017

1018