



HAL
open science

Beyond forest succession: a gap model to study ecosystem functioning and tree community composition under climate change

Xavier Morin, Harald Bugmann, François de Coligny, Nicolas Martin-StPaul, Maxime Cailleret, Jean-marc Limousin, Jean-marc Ourcival, Bernard Prevosto, Guillaume Simioni, Maude Toigo, et al.

► To cite this version:

Xavier Morin, Harald Bugmann, François de Coligny, Nicolas Martin-StPaul, Maxime Cailleret, et al.. Beyond forest succession: a gap model to study ecosystem functioning and tree community composition under climate change. *Functional Ecology*, 2021, pp.1-69. 10.1111/1365-2435.13760 . hal-03084037

HAL Id: hal-03084037

<https://hal.science/hal-03084037>

Submitted on 20 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

1 **Title: Beyond forest succession: a gap model to study ecosystem functioning and tree**
2 **community composition under climate change**

3

4 **Authors:** Xavier Morin^{1,‡}, François de Coligny², Nicolas Martin-StPaul³, Harald Bugmann⁴,
5 Maxime Cailleret⁵, Jean-Marc Limousin¹, Jean-Marc Ourcival¹, Bernard Prevosto⁵,
6 Guillaume Simioni³, Michel Vennetier⁵, Joannès Guillemot^{6,7,8}

7

8 **Authors' affiliations:**

9 ¹ CEFE UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier -
10 EPHE, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France.

11 ² AMAP UMR931, Botany and Computational Plant Architecture, Université de Montpellier –
12 CIRAD – CNRS – INRAE - IRD, TA A-51/PS2, Boulevard de la Lironde, 34398 Montpellier
13 Cedex 5, France

14 ³ INRAE, URFM, , Domaine Saint Paul, INRAE Centre de recherche PACA, 228 route de
15 l'Aérodrome, CS 40509, Domaine Saint-Paul, Site Agroparc, France

16 ⁴ Forest Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, CH-8092 Zürich,
17 Switzerland

18 ⁵ INRAE Aix-en-Provence, Aix Marseille Université, UMR RECOVER, 3275 route de
19 Cézanne CS 40061, 13182 Aix-en-Provence Cedex 5, France

20 ⁶ CIRAD, UMR Eco&Sols, Montpellier, France

21 ⁷ Eco&Sols, Univ Montpellier, CIRAD, INRAE, IRD, Montpellier, SupAgro, Montpellier,
22 France

23 ⁸ Department of Forest Sciences, ESALQ, University of São Paulo, Piracicaba, São Paulo,
24 Brazil

25

26 [‡] To whom correspondence should be addressed.

27 CEFE UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier –
28 EPHE
29 1919, route de Mende
30 F-34293 Montpellier cedex 5 - France
31 Phone: +33 467 61 32 89
32 Fax: +33 467 61 33 36
33 E-mails: xavier.morin@cefe.cnrs.fr

34

35 ***Authors' contributions:***

36 XM conceived the original idea. FdC and XM implemented the model in the CAPSIS
37 platform, benefited from the Forclim model by HB. JG and XM designed the general
38 methodology, and NM carried-out the trait-based analysis. BP, MC, MV, GS, NM, JML and
39 JML provided part of the data. JG and XM analysed the results and led the writing of the
40 manuscript. All authors contributed critically to the drafts and gave final approval for
41 publication.

42

43 ***Acknowledgements***

44 The authors wish to thank the Institut Géographique National for providing the national forest
45 inventory data, and the Office National des Forêts and the RENECOFOR team, particularly
46 Manuel Nicolas and Marc Lanier, for providing their database. In both cases, these long-term
47 monitoring networks are invaluable tools. The SAFRAN database was provided by Météo-
48 France. The authors are also grateful to the CAPSIS modelling platform
49 (<http://www7.inra.fr/capsis/>). They thank Maude Toigo, Georges Kunstler and Patrick Vallet
50 for helpful discussions about the study, and Gregor Cresnar from the Noun Project. This study
51 was funded by the projects BIOPROFOR (ANR-11-PDOC-030-01), DISTIMACC (ECOFOR-

52 2014-23), French Ministry of Ecology and Sustainable Development, French Ministry of
53 Agriculture and Forest) and DIPTICC (ANR-16-CE32-0003).

54

55 ***Data availability statement***

56 The observed and simulated data that support the findings of the study will be deposited in
57 Figshare.

58

59

60 **ABSTRACT**

61 Climate change impacts forest functioning and dynamics, and large uncertainties remain
62 regarding the interactions between species composition, demographic processes, and
63 environmental drivers. There are few robust tools available to link these processes, which
64 precludes accurate projections and recommendations for long-term forest management. Forest
65 gap-models present a balance between complexity and generality and are widely used in
66 predictive forest ecology. However, their relevance to tackle questions about the links between
67 species composition, climate and forest functioning is unclear. In this regard, demonstrating the
68 ability of gap-models to predict the growth of forest stands at the annual time scale –
69 representing a sensitive and integrated signal of tree functioning and mortality risk - appears as
70 a fundamental step.

71 In this study, we aimed at assessing the ability of a gap-model to accurately predict
72 forest growth in the short-term and potential community composition in the long-term, across
73 a wide range of species and environmental conditions. To do so, we present the gap-model
74 ForCEEPS, calibrated using an original parameterization procedure for the main tree species in
75 France. ForCEEPS was shown to satisfactorily predict forest annual growth (averaged over a
76 few years) at the plot level from mountain to Mediterranean climates, regardless the species.
77 Such an accuracy was not gained at the cost of losing precision for long-term predictions, as
78 the model showed a strong ability to predict potential community composition along a gradient
79 of sites with contrasted conditions. The mechanistic relevance of ForCEEPS parameterization
80 was explored by showing the congruence between the values of key model parameter and
81 species functional traits. We further showed that accounting for the spatial configuration of
82 crowns within forest stands, the effects of climatic constraints and the variability of shade
83 tolerances in the species community are all crucial to better predict short-term productivity with
84 gap-models.

85 The dual ability of predicting short-term functioning and long-term community
86 composition, as well as the balance between generality and realism (i.e., predicting accuracy)
87 of the new generation of gap-models may open great perspectives for the exploration of the
88 biodiversity-ecosystem functioning relationships, species coexistence mechanisms, and the
89 impacts of climate change on forest ecosystems.

90

91 INTRODUCTION

92 Forests cover about 30% of the land at the global scale, harbor most of terrestrial biodiversity,
93 are an important carbon sink (Pan et al. 2011), play a pivotal role for climate regulation (Chapin
94 et al. 2008) and provide key ecosystem services to humans (TEEB 2010). However, climate
95 change puts forests at high risk, including disruption in forest dynamics (McDowell et al. 2020),
96 as harsher environmental conditions strongly impact forest structure and composition
97 (Esquivel-Muelbert et al. 2019) and functioning (Boisvenue and Running 2006, Allen et al.
98 2010, Lindner et al. 2010). In turn, compositional changes have been shown to affect forest
99 functioning (Nadrowski et al. 2010, Liang et al. 2016), in interaction with climatic drivers
100 (Coomes et al. 2014, Jactel et al. 2018). Yet, we lack robust tools to explore the interactive
101 effects of biodiversity and climate change on forest dynamics and functioning.

102 Trees are long-lived organisms, which complicates the implementation of experiments
103 designed to assess the influences of future environmental conditions (e.g., increased
104 atmospheric CO₂ (Korner et al. 2005) or water stress (Limousin et al. 2009)) and community
105 composition (including species richness, Castagneyrol et al. 2013, Verheyen et al. 2016) on
106 forest ecosystem functioning. While such experiments are key to study forest ecosystems, they
107 require years to yield relevant results, which are necessarily conditioned by specific site
108 conditions, thereby limiting their generality (Nadrowski et al. 2010, Norby and Zak 2011). An
109 alternative approach lies in the design of field sampling along climate and/or diversity
110 gradients, which has yielded significant results in the last years (e.g., Jucker et al. 2016, del Río
111 et al. 2017, Jourdan et al. 2019), although it can be affected by confounding factors.

112 Complementing these approaches, forest models represent a crucial tool to explore the
113 interactions and feedbacks among species composition, forest functioning and climate
114 (Cordonnier et al. 2018b). Yet, the term « forest models » covers a wide range of approaches,
115 as recently reviewed (Pretzsch et al. 2015, Ruiz-Benito et al. 2020). Forest models were indeed
116 used to predicting forest functioning and growth at scales ranging from tree, to stand (Makela

117 et al. 2000) and landscape (Pacala et al. 1993). Moreover forest models differ in their
118 complexity, from empirical yield tables (Skovsgaard and Vanclay 2008) to ecophysiology-
119 based models (Dufrêne et al. 2005, Simioni et al. 2016) that explicitly describe part of the
120 biological mechanisms at stake but require a large amount of data to be properly calibrated and
121 forced. By contrast, forest gap models (hereafter referred to as “gap models”), operating mostly
122 at the stand scale, rely on empirical relationships, physiological knowledge and first principles
123 from ecological theory (Bugmann 2001). Because these models incorporate physically- or
124 ecologically-based hypotheses while relying on a small set of species-specific parameters, we
125 believe that they are good candidates to explore forest responses to future growing conditions
126 across spatial scales.

127 The design of gap model was originally motivated by the recognition that canopy gaps
128 created by falling trees are a key driver shaping forest structure, dynamics, and succession
129 (Botkin et al. 1972). Although gap models also incorporate representations of abiotic
130 constraints (e.g., water or nutrient stress) on forest functioning, and in some instances
131 competition for belowground resources, their key feature is a representation of the ability of
132 trees of contrasted sizes and different species to compete for light resource. Gap models have
133 been originally developed to understand the processes at play during forest succession (Botkin
134 et al. 1972, Canham et al. 1994, Bugmann 2001). Consequently, they are commonly validated
135 against potential natural vegetation (hereafter “PNV”), or against standing biomass
136 accumulated over long (>50 years) time periods at the tree or stand level (Bugmann 1996,
137 Strigul et al. 2008, Didion et al. 2009, Rasche et al., 2011). Gap models have been used to
138 address a variety of basic and applied research questions, including the effects of climate on
139 forest biomass and composition (e.g., Pfister and Bugmann 2000) or forest management
140 planning (e.g. Rasche et al. 2011, Mina et al. 2017).

141 Recent developments have shown that gap models can be further used to explore species
142 coexistence mechanisms (Chauvet et al. 2017), diversity effects on the functioning of forest
143 ecosystems (Morin et al. 2011, Bohn and Huth 2017) and their response to climate change
144 (Morin et al. 2018). These new perspectives highlight the importance of forest structure and
145 light-related interactions for forest functioning. In fact, forest structure has been shown to
146 influence forest growth (Hardiman et al. 2011, Gough et al. 2019) and to partly mediate tree
147 diversity effects on productivity (Dănescu et al. 2016, Cordonnier et al. 2019, Schnabel et al.
148 2019). Enhanced canopy space occupation ('canopy packing', Jucker et al. 2015) and light
149 capture, which is mediated by the coexistence of species with contrasting shade tolerance, was
150 shown to be key in the functioning of diverse and structurally complex forests (Williams et al.
151 2017). The presence of shade-tolerant species in tree species mixtures indeed strongly
152 modulates the way tree diversity affects forest functioning and productivity (Toïgo et al. 2018,
153 Van de Peer et al. 2018, Cordonnier et al. 2018a). Gap models can be parameterized for a wide
154 range of species and environmental conditions, and could thus be a crucial tool to explore how
155 differences in shade-tolerance affect the relationships between species richness and forest
156 functioning (Morin et al. 2011, Toïgo et al. 2018). However, the multi-dimensional
157 configuration of crowns in forest stands is not often represented explicitly in gap models (but
158 see Maréchaux and Chave 2017, Pacala et al. 1993, Purves et al. 2008), which hinders the
159 assessment of the importance of architectural plasticity and canopy packing on forest
160 productivity, species succession and coexistence.

161 Moreover, exploring Biodiversity-Ecosystem Functioning (BEF) relationships or
162 species coexistence under climate change using gap models will require to assess (i) whether
163 they are able to predict key patterns linking forest composition and functioning and (ii) whether
164 they embed a sound representation of the underlying mechanistic processes. Annual tree growth
165 was shown to be a sensitive and integrated signal of tree functioning and mortality risk

166 (Dobbertin 2005, IFN 2016, Cailleret et al. 2017, DeSoto et al. 2020), in contrast to PNV and
167 standing biomass, which result from the accumulated effects of multiple ecological processes
168 (e.g. tree recruitment, growth and mortality). Demonstrating the ability of gap models to predict
169 the growth of forest stands at the annual time step or across a few years (i.e., to predict biomass
170 *fluxes* in addition to biomass *stocks*; Guillemot et al., 2017), would open important research
171 avenues to investigate how the mechanisms underlying BEF-relationships shape forest
172 dynamics and community assembly (Cordonnier et al. 2018b). In addition, progress in trait-
173 based ecophysiology has allowed identifying key functional traits involved in tree survival and
174 growth in contrasting environments (Falster et al. 2018). Testing the congruence between key
175 model parameters and functional traits is thus another way to evaluate the mechanistic relevance
176 of these models.

177 Here, we aim to test whether a gap model can predict the annual growth of forests
178 differing widely in species composition and climatic conditions throughout France, using only
179 a small set of parameters that can be calibrated based on forest inventories. French mainland
180 forests are found in a wide range of conditions including mountain, continental, oceanic and
181 Mediterranean climates (Verkerk et al. 2019) and are therefore ideal to evaluate the generality
182 of the hypotheses embedded in models. We present the ForCEEPS model (Forest Community
183 Ecology and Ecosystem Processes), derived from ForClim (Bugmann 1996, Didion et al.
184 2009). Among other novelties, ForCEEPS embeds an improved representation of tree-tree
185 competition for light by considering individual crown sizes in the vertical canopy space.
186 ForCEEPS was parameterized for the main French tree species, and evaluated against annual
187 growth (averaged across a few years) at the tree and stand scale, and against PNV. In addition,
188 we verified the mechanistic relevance of ForCEEPS by assessing the congruence of key species
189 parameters with functional traits. Finally, we conducted a sensitivity analysis on the ForCEEPS
190 stand growth predictions, to quantify the importance of 1) an explicit representation of crown

191 size, 2) the variability of shade-tolerance among species, and 3) the climatic constraints for
192 accurately simulating stand growth.

193

194 **MODEL DESCRIPTION**

195 **Overview**

196 The ForCEEPS model is a forest gap model (also called forest dynamics model). Forest gap
197 models simulate abiotic (climate and soil properties) and biotic constraints (tree-tree
198 competition for light) on tree establishment, growth, and survival in small parcels of land
199 (“patches”). The mechanisms embedded in gap models rely on ecological hypotheses clearly
200 stated, such as the trade-off between growth in full light and survival under shade (Bazzaz
201 1979). Tree height and crown dimensions are inferred from allometry, based on tree trunk
202 diameter, which is also the main variable measured in forestry surveys. Gap models commonly
203 simulate forest dynamics at an annual time step, and do not explicitly represent biogeochemical
204 cycling. ForCEEPS shares many features with the JABOWA (Botkin et al. 1972) and ForCLIM
205 models (Bugmann 1996), and more precisely with ForCLIM 2.9.6 (Didion et al. 2009). Below,
206 we present the central principles of ForCEEPS and the key developments that differentiate it
207 from other gap models (a full description of the model is provided in Appendix A).

208 The simulated patches are independent from each other, and properties at the forest level
209 are obtained by aggregating the properties over all patches (Shugart 1984, Bugmann 2001).
210 Within each patch (i.e., usually between 400 and 1000 m²), environmental conditions are
211 assumed to be horizontally homogeneous. The spatial location of trees is therefore implicit, and
212 the competitive ability of a tree is assumed equal for all trees of similar size and species. This
213 hypothesis allows for several simplifications in the representation of tree-tree interactions, but
214 imposes that the patch size cannot be larger than 1000 m², which is assumed to be the maximum
215 area influenced by a tree (Shugart 1984). Gap models are often cohort-based, assuming that all

216 trees of the same species and age behave similarly, for the sake of simulation efficiency. By
217 contrast, ForCEEPS is completely individual-based, which notably allows to simulate the
218 intraspecific variability in competitive ability. Another novel aspect in ForCEEPS is the
219 possibility of imposing a feedback between the actual forest composition and the identity of the
220 colonizing seedlings each year. This latter feature may be crucial for examining mechanisms of
221 species coexistence in tree communities (Cordonnier et al. 2018b). However, with regard to the
222 objective of the present paper, the most crucial development of ForCEEPS in comparison with
223 ForClim is the implementation of a new module for tree-tree competition for light, i.e. a key
224 factor controlling growth and forest structure (Schwinning and Weiner 1998), where the
225 individual crown lengths are explicitly represented in the vertical canopy space (see Appendix
226 A).

227 Tree establishment, growth, and mortality are simulated at a yearly time step, but
228 monthly climatic data (monthly mean temperature and precipitation sum) are used to estimate
229 annual or seasonal degree-days sum (*GDD*), winter temperatures, and a drought index (*DrI*).
230 The latter depends on monthly soil water content (*SWC*) that is calculated from a monthly water
231 budget (Bugmann and Solomon 2000) and is influenced by the site-specific maximum soil
232 water holding capacity. Last, soil nutrients content (N_{soil}) is another abiotic factor simulated in
233 ForCEEPS, considered constant at the site level (Appendix A).

234

235 **Seedling establishment**

236 Seedlings are established with a diameter at breast height of 1 cm. Establishment success is
237 simulated as a function of species-specific responses to *DrI*, *GDD*, winter temperature (see
238 Table 1 for species parameter description, and Appendix A), light availability at the forest floor
239 (see *realized tree growth* section), and browsing pressure (Didion et al. 2011). By default, the
240 model assumes that there is a constant seed rain in the patches and thus no dispersal limitation,

241 but alternatively it is possible to activate a feedback between the actual forest composition at
242 year n and species composition of the new seedlings at year $n+1$. Seedling establishment can
243 be constrained by defining a maximum number of seedlings potentially colonizing the patches
244 and/or by imposing a feedback of actual forest composition on the composition of colonizing
245 seedlings (Appendix A).

246

247 **Tree mortality**

248 Tree mortality depends on two components: (i) a “background” mortality that is constant across
249 time, and (ii) a growth-related mortality (Appendix A). The background mortality is purely
250 stochastic. It depends on species’ maximum longevity and simulates mortality events induced
251 by ‘random’ small-scale disturbances (e.g., attack of pathogen in an endemic phase). Large-
252 scale disturbances (e.g., windthrows, wildfires) can be taken into account by increasing the
253 background mortality rate, but are not considered here. The growth-related mortality is a proxy
254 for stress conditions, i.e., tree mortality probability increases with the decrease in absolute or
255 relative tree growth (i.e. tree vigor) induced by abiotic factors or by competition (DeSoto et al.
256 2020). It is thus noteworthy that competition has an indirect effect on mortality rates via the
257 growth-related mortality.

258

259 **Potential tree growth**

260 Annual tree growth is modelled through stem diameter increment at breast height (ΔD).
261 Following the classical scheme of gap models, ΔD is calculated in two steps. First, the potential
262 (i.e. maximum) diameter increment (ΔD_{opt}) of each tree is predicted in each year using the
263 following empirical equation (Moore 1989):

$$264 \quad \Delta D_{opt} = g_s \frac{D \left(1 - \frac{H}{H_{max_s}} \right)}{2. H_{max_s} - b_s \times e^{(c_s \cdot D) \times (c_s \cdot D + 2)}} \quad (\text{Eq. 1})$$

265 where D is tree diameter at breast height, H is tree height, g_s is the maximum growth
 266 rate of species s , H_{max_s} is the maximum height reachable by the species s , and b_s and c_s are
 267 species-specific parameters (with $b_s = H_{max_s} - 137$; and $c_s = S_s / b_s$); s_s is a species-specific
 268 allometric parameter relating tree height and diameter as follows (Bugmann 1996):

$$269 \quad H = a + (H_{max_s} - a) \times \left(1 - e^{\left(\frac{-S_s \cdot D}{H_{max_s} - a} \right)} \right) \quad (\text{Eq. 2})$$

270 with $a = 1.37$ m (i.e. breast height). Therefore, simulating the potential diameter
 271 increment of a tree in ForCEEPS requires to determine the values of the species-specific
 272 parameters g_s , s_s and H_{max_s} (Table 1).

273

274 **Realized tree growth**

275 Realized tree diameter increment ΔD is calculated by modifying ΔD_{opt} according to abiotic or
 276 biotic growth reduction factors (all factors are bounded between 0 and 1) following a modified
 277 geometric mean (Bugmann 1996, Didion et al. 2009):

$$278 \quad \Delta D = \Delta D_{opt} \times \sqrt[3]{GR_{light} \times GR_{gdd} \times GR_{drought} \times GR_{soil}} \quad (\text{Eq. 3})$$

279 where GR_{light} is the growth reduction factor related to light availability for the tree, GR_{gdd} is the
 280 growth reduction factor related to growing season temperatures of the site (GDD), $GR_{drought}$ is
 281 the growth reduction factor related to the site drought index (DrI), and GR_{soil} is the growth
 282 reduction factor related to soil nutrients content (N_{soil}) (see Appendix A). The effects of each of
 283 these growth reduction factors on realized tree growth depend on species-specific parameters:
 284 GR_{light} depends on species shade tolerance ShT_s ; GR_{gdd} depends on species minimum sum of
 285 growing degree-days GDD_s ; $GR_{drought}$ depends on species drought tolerance DrT_s ; and GR_{soil}
 286 depends on species requirements for soil nutrients $NReq_s$ (see Table 1). All growth reduction
 287 factors vary among site conditions and species, and GR_{light} varies also among trees, because it
 288 is influenced by the sizes of the neighbouring trees in the patch (see next section).

289

290 **Effects of the competition for light on tree growth**

291 In ForClim 2.9.6 (Didion et al. 2009), the amount of light available for a tree (with H being its
292 total height) is reduced by the leaf area of the trees found in the same patch whose height is
293 greater than H or equal to H . Thus, all the foliage of trees taller than the target tree contribute
294 to the shading. ForCEEPS embeds a more realistic description of the competition for light, by
295 representing individual crown lengths in the vertical space of the canopy (Fig. S1 and Appendix
296 A).

297 In ForCEEPS, the growth reduction factor related to light availability (GR_{light}) has two
298 components:

299
$$GR_{light} = GR_{cs} \times GR_{sh} \quad (\text{Eq. 4})$$

300 with GR_{cs} representing the feedback of crown size on tree growth, i.e., tree leaf area is positively
301 linked to tree growth rate (Mitscherlich and von Gadow 1968). GR_{sh} is the reduction factor
302 related to shading by competing trees. The key feature is that individual tree crowns are
303 characterized by crown length cl , calculated as follows for each tree i :

304
$$cl_i = cs_i \times H_i \quad (\text{Eq. 5})$$

305 with H being tree height and cs being the ratio of the height with a green crown, which is related
306 to light exposition of the tree (Didion et al. 2009). For each tree, cs varies between two extreme
307 species-specific values that represent the case where the tree is fully shaded ($cs = cs_{min_s}$) or
308 in full light ($cs = cs_{max_s}$), with:

309
$$cs_i = cs_{max_s} - (cs_{max_s} - cs_{min_s}) \times k_{LAI} \quad (\text{Eq. 6})$$

310 where the extreme values cs_{max_s} and cs_{min_s} have been derived from the relationship between
311 foliage fresh weight and DBH described in Wehrli et al. (2007) and depends on the foliage type
312 parameter f_S (see Appendix A), and k_{LAI} is the correction factor - ranging from 0 (no shading)
313 to 1 (full shading) - calculated by Didion et al. (2009) as follows:

314
$$k_{LAI_i} = \min \left[\left(\frac{LAI_{H_i}}{LAI_{max}} \right)^2, 1 \right] \quad (\text{Eq. 7})$$

315 with LAI_H being the cumulative double-sided leaf area index between the top of the canopy and
316 the top of the target tree (i.e. between the top of the canopy and the height H) and LAI_{max} being
317 the maximum value of double-sided leaf area index in a patch, resulting from the light
318 compensation point of the most shade-tolerant European tree species [i.e. $LAI_{max} = 11.98$
319 (Bugmann 1994, Didion et al. 2009)].

320 The vertical space of the patch p at simulation step $t=t_1$ is discretized in $n(p, t_1)$ layers of
321 a given width w , whose value is bounded between 0 (ground level) to $H_{max}(p, t_1)$ (height of
322 the tallest tree in the patch p at $t=t_1$), with $w = 1$ m. We assumed that tree leaf area decreases
323 linearly from the top to the base of the crown, i.e. from the highest to the lowest layer in which
324 the crown of the tree is found (Fig. S1-B) (Eermak 1998, Van Pelt et al. 2016). We are aware
325 that tree crown shape and vertical leaf area distribution vary among tree species and are also
326 affected by the size and identity of neighbouring trees (Poorter et al. 2006, Williams et al. 2017,
327 Niklaus et al. 2017). Our assumption should thus be seen as a first parsimonious step that can
328 be refined using species- and context-specific architectural data. Further details about the
329 calculation of GR_{cs} and GR_{sh} are described in Appendix A.

330

331 **Effects of the environmental conditions on tree growth**

332 Belowground competition for water and nutrients is not explicit in ForCEEPS. However, while
333 the model focuses on competition for light in its current version, it is noteworthy that soil
334 nutrient content and soil moisture indirectly affect competition for light, in a way that differs
335 among species (Table 1). In fact, GR_{soil} and $GR_{drought}$ affect tree dimensions (diameter and
336 height) (Eq. 3) and thus tree leaf area (Eq. 11), which in turn modifies the competitive ability
337 of a tree because shading directly depends on leaf area (Eq. 12). Therefore, site conditions (soil
338 and climate) modulate competition among trees.

339

340 CALIBRATION, VALIDATION, AND SENSITIVITY ANALYSIS

341

342 Species

343 The calibration and validation of ForCEEPS was done for nine species (Table S1) - four
344 Angiosperm species and five Gymnosperm species, including the seven most widespread tree
345 species in France (*Quercus petraea*, *Q. robur*, *Fagus sylvatica*, *Abies alba*, *Picea abies*, *Pinus*
346 *sylvestris* and *P. pinaster*) (IGN 2018), and two emblematic species of Mediterranean French
347 forests (*Pinus halepensis* and *Quercus ilex*). Furthermore, *P. pinaster* is the planted species
348 covering the largest area in France. These species dominate in contrasted stages of the
349 vegetation succession: pioneer (*Pinus*), intermediate- (*Picea*) or late-succession species
350 (*Quercus*, *Fagus*, *Abies*).

351 Furthermore, for the PNV simulations, we complemented the set of studied species by
352 considering 13 additional species ('*other species*' in Table S1) to cover most possible forest
353 types: *Acer campestre*, *A. platanoides*, and *A. pseudoplatanus* (grouped in "Acer" species);
354 *Larix decidua* and *Pinus cembra* (grouped in "mountain gymnosperms"); *Sorbus aria*, *S.*
355 *aucuparia*, and *Ulmus glabra* (grouped in "mountain broadleaves"); *Betula pendula*, *Fraxinus*
356 *excelsior* and *Populus tremula* (grouped in "other broadleaves" species); *Carpinus betulus*, and
357 *Quercus pubescens*. However, no forest growth data was available to properly calibrate or
358 validate the model for these other species as done for the nine main ones. This notably occurred
359 because growth data at the stand scale were not available for these species (see Validation
360 section) and growth data at the tree scale were only available for *C. betulus* and *Q. pubescens*
361 (see Table S2).

362 The workflow of the study is summarized in Fig. 1.

363

364 **Calibration**

365 Each species simulated in ForCEEPS is defined by 13 key parameters described in Table 1 (and
366 Table S1) from which other parameters were derived (b_s and c_s in Eq. 1, f_s and a_s in Eq. 11,
367 cS_{min_s} , cS_{max_s} in Eq. 6, LCP_s in Eq. 8). The variability among functional traits reflects
368 fundamental trade-offs of species life-history strategies (Bazzaz 1979, Violle et al. 2007). In
369 ForCEEPS, like in many gap models, the variability among parameters' values aims at
370 reflecting such trade-offs (Bugmann 2001), and in this sense we further assume that the
371 parameters describing the species in the model are proxies of life-history or functional traits.
372 For instance, late-successional species are generally characterized by slow growth (i.e. low
373 values of g_s), long lifespan (i.e. low values of $Amax_s$), and high shade tolerance (i.e. low values
374 of $ShTol_s$), in contrast to early-successional ones (Reich 2014).

375 In the present study, the calibration of potential tree growth (i.e., species-specific
376 parameters g_s and H_{max_s}) and the allometry relating tree height and diameter (i.e., parameter
377 s_s) were based on data from the French National Forest Inventory (NFI) (IGN 2018). The values
378 of other parameters were based on the literature. The NFI sampling design warrants an
379 exhaustive representation of environmental gradients within the realized distribution of the
380 species over the mainland French territory, while individual plots may not be locally
381 representative (Charru et al. 2010). Therefore, we used NFI to calibrate the potential growth
382 model in ForCEEPS, but did not use it for the validation at the plot level. More detailed
383 information about NFI data is available in Appendix D.

384

385 *Parameter g_s .* This parameter is the most difficult to calibrate as it requires data from trees
386 growing in “optimal conditions”, which are scarce in observational datasets as the growth of
387 trees is usually constrained by environmental conditions or biotic factors (e.g. competition). To
388 cope with this challenge, we took advantage of the NFI that covers a very wide range of

389 conditions (in both space and time), providing a large number of “annual diameter increment
390 vs. diameter” pairs for each of the 11 species (i.e., the nine main species and *C. betulus* and *Q.*
391 *pubescens*) for which abundant data were available (n=206,569 for all species confounded,
392 Table S2). For each of these 11 species, we grouped trees according to their diameter (according
393 to 1-cm size classes) and selected the 10% of trees with the greatest annual diameter increment,
394 assuming that these trees grew in “optimal conditions” or at least under almost unconstrained
395 conditions. However, we note that the annual increments are derived from five-year average,
396 which may lead to an underestimation of the actual greatest annual diameter increments. Then
397 we fitted g_s from Eq. 1 with this dataset, using a non-linear least squares approach implemented
398 by the `nls` function in the R software (R Core Team 2018). For the remaining species (n = 11),
399 the g_s values have been set from previous studies (Didion et al. 2009).

400 The fitted values for the parameters g_s ranged from 79 to 399 (Table S1). These values
401 are consistent with former estimates for the same or related species (Bugmann 1994, Didion et
402 al. 2009).

403

404 *Parameter s_s .* The calibration of s_s (Eq. 2) relied on NFI data because of their representativeness
405 of the conditions in which each species occurs. The whole NFI dataset was used for the
406 calibration to cover the largest range of conditions in which each species occurs. Although
407 diameter-height relationships were shown to be affected by environmental conditions, e.g.
408 climate, tree social status and stand density (Trouvé et al. 2015, Fortin et al. 2019), these factors
409 were not accounted for in the model. The rationale for this lies in our aim to keep the model
410 structure as simple as possible to allow for an easy parameterization and use at large scale for
411 a large number of species. We fitted the height-diameter relationships (Eq. 2) on the NFI
412 dataset, using the `nls` R function, and extracted s_s values for each species. As for g_s , this

413 calibration was conducted for the 11 main species, while we relied on Didion et al. (2009) for
414 the 11 additional species.

415

416 *Parameter H_{max_s} .* This parameter was calibrated using NFI data and/or literature (Rameau et
417 al. 1989, 2008) for all the species. Maximum height may indeed be underestimated in the NFI
418 data because forest managers tend to harvest the largest trees before they reach their maximum
419 height.

420

421 *Other parameters.* The values of the parameters describing species' response to abiotic
422 conditions (i.e. effect of the growing season temperature on tree growth, $DDmin_s$; drought
423 tolerance, $DrTol_s$; and soil nitrogen requirement, $Nreq_s$), and species intrinsic characteristics
424 (i.e. foliage type, f_s ; maximum age, $Amax_s$, shade tolerance, $ShTol_s$, and shade tolerance of
425 seedlings $ShTol_seedling_s$, browsing susceptibility of seedlings Br_s) were based on the literature
426 (Table 1 and references therein). Parameters describing the thermal regeneration niche for
427 seedlings (i.e., monthly minimum and maximum winter temperature tolerated for regeneration
428 $WTmin_s$ and $WTmax_s$, Table 1) were calibrated according to species-specific diagrams of
429 occurrence (San-Miguel-Ayanz et al. 2016).

430

431 *Congruence of key parameter values with functional traits.*

432 To gain mechanistic insight into the parameters values derived from the calibration procedure,
433 we evaluated the congruence of key model parameters with functional traits extracted from the
434 literature. To do so, we first selected the most meaningful ForCEEPS parameters in terms of
435 species ecological strategies, including g_s , $DrTol_s$, $ShTol_s$, $ShTol_seedlings_s$, and $Nreq_s$. Then
436 we collected data on relevant traits from various database, including: xylem cavitation
437 resistance (assess through the water potential causing 50% cavitation, ψ_{50} in MPa), leaf turgor

438 loss point (ψ_{tlp} , in MPa), water potential causing stomatal closure (ψ_{close} , in MPa) and safety
439 margins from ψ_{tlp} and ψ_{close} [from the SurEAu database, Martin-StPaul, Delzon, & Cochard
440 (2017)], wood density (g/m^3 , Chave et al. 2009), light saturated CO₂ assimilation (or maximal
441 photosynthesis A_{max} , in $\mu\text{mol/m}^2/\text{s}$), nitrogen content per unit leaf area N_a (g/m^2) and leaf mass
442 per area LMA (g/m^2) [from the CANTRIP database, Keenan & Niinemets (2016)]. The final
443 trait database and associated references are reported in Appendix E. For each of the selected
444 ForCEEPS parameters, we tested the Pearson's correlations between the ForCEEPS parameters
445 and some of the traits at the interspecific level. Note that the consistence of the results across
446 both Angiosperms and Gymnosperms was taken into account to assess the robustness of the
447 congruence of species parameters with functional traits.

448

449 **Validation against forest growth data**

450 *Forest growth dataset.* The validation of simulated annual productivity at the tree and stand
451 levels was conducted using a dataset independent from the one used in the calibration process.
452 Following Guillemot et al. (2017), we primarily relied on the RENECOFOR permanent forest
453 plot network (Ulrich 1997) that includes 103 half-hectare plots in even-aged managed forests
454 covering most of the main tree species and climate conditions in France. After excluding the
455 plots that had experienced a natural or anthropic disturbance (e.g., thinning) less than 4 years
456 before the last diameter inventory, 77 plots remained. Most of the stands included in the
457 validation dataset are monospecific or strongly dominated by one species

458 The RENECOFOR network does not include forests growing under Mediterranean
459 conditions. Therefore, we completed the validation by using data from the long term
460 experimental sites of Puéchabon (*Quercus ilex*, Rambal et al. 2014) and Font Blanche (mixed
461 forest dominated by *Pinus halepensis*, Simioni et al. 2016). Diameter inventories were used to
462 estimate the tree and stand basal area increment (BAI) in all validation plots. The time interval

463 between the initial and final inventories in RENECOFOR plots varied between 4 and 14 years,
464 while they were of 14 and 10 years for the Puéchabon and Font Blanche sites, respectively (see
465 further details about the validation datasets in Appendix D). The BAI data recorded over
466 contrasted time intervals were normalized to mean annual BAI. Local measurements of soil
467 water holding capacity (SWHC) were available for all plots, and climate time-series were
468 obtained from the SAFRAN atmospheric reanalysis (Vidal et al. 2010) for the RENECOFOR
469 plots, and from on-site measurements for the Puéchabon and Font Blanche plots. The validation
470 plots covered a large range of environmental conditions, with mean annual temperature (*MAT*)
471 ranging between 5.8°C and 14.3°C, mean annual precipitation sum (*MAP*) between 700 and
472 2030 mm, while the drought index ranged from 0.003 to 0.35 (values below 0.05 indicate there
473 is no marked drought stress for the trees, while values above 0.3 indicate strong stress for most
474 tree species) (Fig. S2).

475

476 *ForCEEPS simulations.* We initialized the model for each stand using the first inventory
477 campaign of the respective plot. For each RENECOFOR plot, 5 patches of 1000 m² were
478 simulated, in order to obtain comparable observed and simulated forest plot areas (the
479 average size of the observed plots is ca. 5000 m²). To simulate the patches, trees were randomly
480 sampled in the inventory dataset of a given plot until the stand basal area per square meter of
481 the simulated patch was comparable to the observed stand basal area per square meter. Local
482 measurements of SWHC and local climate time-series were used as inputs. ForCEEPS
483 simulations were run over the time period for which BAI measurements were available in each
484 plot (i.e. from 4 to 14 years), and subsequently normalized to mean annual BAI. As the results
485 were very consistent across the five repetitions carried out per plot (as shown in Fig. S3 for the
486 RENECOFOR plots), we only present the results for one repetition at the tree level for the sake
487 of clarity (the results for each repetition are shown in supplementary material - Table S4 and

488 Fig. S3). For results at stand level, we present averages across the five repetitions (the results
489 for each repetition are shown in supplementary material - Table S4).

490 Gap models like ForCEEPS are designed to explore processes occurring at the stand
491 level and are thus more relevant at this scale. However, as neighborhood interactions are
492 reported to be key in driving BEF relationships and for the sake of comprehensiveness, we also
493 present the results at the tree level (Schnabel et al. 2019, Jourdan et al. 2019a).

494

495 **Quantifying the importance of the hypotheses embodied in ForCEEPS for forest growth**

496 After simulating BAI for each plot using the full model, we carried out three types of
497 simulations to quantify the importance of some hypotheses and ecological processes embedded
498 in ForCEEPS. First, we ran simulations without the new module for competition for light, to
499 test whether an explicit representation of individual crown lengths in the vertical canopy space
500 increased the prediction accuracy of stand growth (*Test 1*). Second, we ran simulations without
501 considering the limiting effect of drought stress and thermal constraints on tree growth, i.e.
502 under optimal climatic conditions (*Test 2*). Third, we aimed at testing the importance of the
503 species-specific tolerance to shade in ForCEEPS (*Test 3*), as it has been shown to be a key
504 parameter driving diversity effects in ForClim 2.9.6 (Morin et al. 2011). To do so, we changed
505 the specific values of the parameter *ShTol_S* by assigning the maximum value to all species. Note
506 that this kind of tests has been rarely done with gap models [but see (Morin et al. 2011, Huber
507 et al. 2018)].

508

509 **Validation against potential natural vegetation**

510 *Study sites.* To validate the model's predictions in terms of outcomes of climate effects and
511 interspecific competition in the long term, we compared the community composition simulated
512 by ForCEEPS with the tree species composing the potential natural vegetation (PNV) along an

513 environmental gradient. Defining PNV for a given site is subject to personal judgment. Here,
514 similarly as in Bugmann (1996), we simply relied on the assumed dominant tree species
515 (assuming no large disturbances) in a space spanned by annual precipitation (*MAP*) and mean
516 annual temperature (*MAT*), following Ellenberg (1986), Rameau et al. (1989, 2008) and San-
517 Miguel-Ayanz et al. (2016) (Fig. 4-B). More precisely, we selected 14 sites with contrasted
518 conditions among the 79 plots used for the validation of forest growth simulations. This gradient
519 thus includes dry and warm conditions through the two Mediterranean sites, but it did not
520 include the coldest conditions in which forests can grow in France. Therefore we added another
521 site with average MAT of 2.9°C (± 0.64) and ASP of 1577 mm (± 253), corresponding to the
522 conditions of a subalpine site according to Ellenberg (1986) (grey dot in Fig. S2, and site 1 in
523 Fig. 4-B).

524

525 *ForCEEPS simulations.* For each of the 15 sites, we ran 2500-yr simulations, starting from bare
526 ground. Thus, the PNV simulations accounted for seedling establishment, tree growth and
527 mortality. This simulation duration was necessary to avoid the communities to be in a transient
528 phase and to ensure that they reached a pseudo-equilibrium in terms of composition and basal
529 area. The 2500-yr climate time-series were obtained by randomizing the years from which time-
530 series were available for each site. In other words, we considered inter-annual variability in
531 climate, but there was no trend in the long term, as commonly done in studies aiming at
532 depicting forest succession with gap models (e.g., (Bugmann 1996, Morin et al. 2011, Chauvet
533 et al. 2017). We considered 200 patches of 1000 m² for each simulation. At the end of the
534 simulation, we extracted the mean basal area per hectare of the simulated stands and the basal
535 area of each species.

536 The performance of the model was assessed using Pearson correlation coefficient (r),
537 the root mean square error (RMSE), and the average bias (AB) between observations and model
538 predictions.

539

540 **RESULTS**

541 **Prediction of aboveground tree growth.**

542 ForCEEPS was able to capture the observed mean annual BAI (Fig. 2) at the tree level, with a
543 good correlation between observations and predictions ($r=0.72$, $n=2662$; Table 2), while the
544 difference between observations and predictions was satisfactory (RMSE = 0.0012, AB =
545 12.4%). There was, however, a slight tendency to underestimate the growth of the most
546 productive trees (Fig. 2), and the uncertainty of the model predictions increased with tree
547 diameter (Fig. S6). When the species were examined separately, the Pearson correlation
548 coefficient ranged from 0.49 (*P. sylvestris*) to 0.77 (*F. sylvatica*) (Table 2, Fig. S4) but the
549 difference between observations and predictions strongly varies between species (RMSE =
550 0.0013 and AB = 21.8%, on average).

551

552 **Prediction of aboveground stand growth.**

553 At the stand level, ForCEEPS showed a good ability to reproduce observed mean annual BAI
554 regardless of the species or the environmental conditions. Across all plots, the correlation was
555 strong between observations and predictions ($r=0.79$, $P<0.001$, Table 3) with a very low
556 difference between observations and predictions (RMSE = 0.019 and AB=4.5% – Fig. 3-A,
557 Table 3) without strong bias related to the basal area of the stand (Fig. S7). When species were
558 examined separately, the accuracy varied across species, but the results did not show strong
559 systematic bias (Fig. S5, RMSE = 0.014 and AB = 26.7% on average, Table 3-b) except for *Q.*
560 *petraea*, for which productivity of the most productive plots was underestimated (RMSE=0.016

561 and AB=-16.7%, Fig. S5), and *P. pinaster*, which showed the highest variability (RMSE=0.034
562 and AB = 50.3%, but it is the species with the smallest number of observations – except *Q. ilex*
563 and *P. halepensis* for which one can hardly make any conclusion with only three plots).

564

565 **The importance of light competition, environmental conditions and shade tolerance for**
566 **simulating forest growth in ForCEEPS.**

567 *Testing the representation of light competition.*

568 The new module for competition for light, which include an explicit representation of individual
569 crown lengths in the vertical canopy space, yielded on average better results than the former
570 version (decrease by 15.4% in RMSE; Table 3-a). The former version tended to underestimate
571 the productivity of the most productive plots, while this was not the case with the new version
572 (Fig. 3-A and 3-B).

573 *Testing the effect of environmental conditions.*

574 The model without climatic constraints on tree growth was less accurate than the full version
575 (increase by 69.7% in RMSE; Fig. 4-A and 4-C; Table 3-a), except for a few plots - especially
576 for *Q. petraea* stands. The simulations without climatic constraints logically tended to
577 overestimate stand productivity (Fig. 3-C). It is thus noticeable that on average, the effect of
578 climatic conditions improved the accuracy of the simulations over such a large range of
579 environmental conditions tested in this study (illustrated in Fig. S2). One may also notice that
580 this improved accuracy is consistent across species, regardless their averaged productivity.

581 *Testing the importance of the variability in the shade tolerance parameter.*

582 When the variability in the ability of species to tolerate shade was not taken into account in
583 ForCEEPS, the model's performance strongly decreased, with an increase in RMSE by 85.11%
584 across plots (Fig. 3-A and 3-D; Table 3-a). The bias notably increased for the most productive
585 stands, especially dominated by *A. alba* and *P. abies* (Fig. 3-D).

586

587 **Prediction of species composition in the long term.**

588 When comparing the distribution of the dominant tree species at the end of the 2500-yr
589 simulations carried out along the environmental gradient covered by the 15 sites (Fig. 4), it
590 appeared that the ability of ForCEEPS to predict reliable PNV varied across sites: the overall
591 likelihood of the simulated communities is strong, but with be a greater uncertainty about
592 Mediterranean forest types. In 10 out of the 15 sites, the dominating species were accurately
593 predicted according to the PNV diagram (green dots in Fig. 4-B). In the five other sites, at least
594 one of the dominating species was accurately predicted (blue dots in Fig. 4-B), while there was
595 no site in which the simulated community was dominated by species other than those expected.

596 Long-term simulation of stand basal area cannot be directly evaluated against field
597 observations as there is no forest stands unaffected by management for several centuries at these
598 sites. Yet, one may notice that the values appear consistent (albeit a bit low) with mature stands,
599 and that the simulated basal area was lower in the harshest conditions (i.e., at both extremes of
600 the gradient). However, the basal area for the Font Blanche site seemed to be underestimated
601 (ca. 15 m²) (Simioni et al. 2016).

602 It is noticeable that the cumulated basal area of the species that were not validated
603 against forest growth data in the present study (ie. the “other species” in Table S1) represent on
604 average only 17% (across the 15 sites) of stand basal area at the end of the simulations, and it
605 remains below 25% at all sites.

606

607 **Congruence of key parameter values with functional traits.**

608 We found correlations between traits and ForCEEPS parameters, but their sign and significance
609 strongly varied. The species nitrogen requirement *Nreq_s* was found to correlate with *Na* (Table
610 S5). The growth parameter *g_s* was significantly negatively correlated with wood density (Figure

611 5), while the correlation with *LMA* was not consistent for Angiosperms and Gymnosperms
612 (Table S5). Seedling and adult shade tolerance were correlated with light saturated
613 photosynthesis (A_{max} , Fig. 5 and Table S5). Other traits, including *LMA* and wood density were
614 poorly correlated with shade tolerance. Finally, correlations were found between *DrTol_S* and
615 different drought-related functional traits. In particular, a strong correlation was found between
616 *DrTol_S* and the stem xylem embolism resistance (assessed by *P50*, i.e., the water potential
617 causing 50% embolism, Fig. 5). The correlation between *DrTol_S* and *P50* was very strong for
618 angiosperms ($r^2=0.7$, $p<0.001$) but not significant for gymnosperms ($p = 0.1$), which could be
619 explain by the fact that the studied conifers all belong to the *Pinaceae* family that rely on a tight
620 stomatal control of transpiration during drought. Positive but less pronounced relationships
621 were found between *DrTol_S* and the turgor loss point (Table S5). *DrTol_S* was also correlated
622 with wood density and *LMA* but to a lower extent (Table S5).

623

624 **DISCUSSION**

625 **A gap model predicting annual productivity and community composition.**

626 ForCEEPS relies on ecological hypotheses, notably the trade-off between maximum growth
627 and tolerance to competition (Rees et al. 2001) and the fact that cyclical succession is occurring
628 in each individual patch (Botkin et al. 1972), allowing to simulate long-term species ecological
629 succession. Although most biogeochemical processes are implicit in the model, as in most gap
630 models, our results show that ForCEEPS accurately predicts both the dominant species
631 occurring at a site in the long term and the wood productivity of monospecific stands across a
632 few years.

633 Gap models have long demonstrated their ability in predicting the long-term dominant
634 species of forests (Bugmann 2001), but it is noticeable that ForCEEPS appeared robust across
635 a large range of environmental conditions, i.e. from alpine to Mediterranean forests. Indeed, if

636 gap models were already shown to accurately predict dominant species composition in
637 temperate and subalpine forests (e.g. Bugmann 1996; Didion et al. 2009), the good
638 performances of ForCEEPS at Mediterranean sites appears as a major achievement. Although
639 this validation remains mostly qualitative, the accuracy of predicted community composition
640 from the long-term simulations is remarkable, and suggests that the interspecific competition
641 and abiotic constraints are well represented in ForCEEPS. The good performances of
642 ForCEEPS across large environmental gradients and for the most important tree species found
643 in mainland France, suggest that the model could be applied to a large part of the European
644 forest ecosystems.

645 The validation of the ability of ForCEEPS to predict forest functioning in the short term
646 (i.e. across a few years) was conducted using forest growth data from monospecific stands. The
647 rationale for this choice was to evaluate its behavior and predictive ability in a context with low
648 influence of complex interspecific interactions. Because gap models are often validated using
649 species composition of PNV at selected sites, their validation is actually conducted in mixed
650 forests in most cases (Bugmann 2001). Thus, this test of the ability of gap models to accurately
651 simulate the functioning of monospecific stands in various environmental conditions and for a
652 wide range of species has been very rarely assessed. Yet, monocultures are often compared to
653 mixed stands to quantify biodiversity effects in forests (e.g., as in Morin et al. 2011). Ensuring
654 that the functioning of monospecific stands is well reproduced by a gap model is thus a *sine*
655 *qua non* condition to simulate non-biased biodiversity effects in tree communities.

656 Validation against forest growth data was rarely done for gap models (Bohn et al. 2014),
657 especially for such a wide range of species and conditions. Gap models have not originally been
658 designed to work at short temporal scales, and are thus not expected to accurately simulate
659 annual tree or stand growth (Mette et al. 2009, Fyllas et al. 2014). Although ForCEEPS may
660 never offer detailed mechanistic insights into ecosystem biogeochemistry and tree growth as

661 ecophysiological models do (Makela et al. 2000, Dufrêne et al. 2005, Guillemot et al. 2017), it
662 can nevertheless be considered as a parsimonious alternative – notably in terms of calibration
663 – to explore how productivity will respond to changes in species composition and climate.

664 Recent advances in forest ecology have resulted in physiological process-based models
665 that can be fully parameterized (e.g. Maréchaux and Chave 2017, Martin-StPaul et al. 2017)
666 using functional traits available from global databases (Kattge et al. 2011). Although these
667 models provide a unique insight on the physiological mechanism driving forest growth and
668 survival, they are not aimed to describe the long-term ecological processes shaping forest
669 composition on the long-term. In this study, we evidence that the processes embodied in gap
670 models to simulate long-term forest succession can also predict annual forest growth in species
671 with contrasted ecology and under various climate conditions, making them an important tool
672 to study forest responses to climate change. ForCEEPS requires a rather small number of
673 parameters to describe a species, allowing both a straightforward calibration of some
674 parameters using forest inventory data and an *a priori*-calibration of the other parameters
675 relying on literature and ecological knowledge. Consequently, the hypotheses embodied in
676 ForCEEPS regarding the complex feedback loops and threshold mechanisms that drive forest
677 functioning and forest community dynamics can be conceptualized, parameterized and
678 evaluated against measured field data. This limits the uncertainty that can affect model
679 predictions in case of equifinality. Of course, ForCEEPS - like all gap models - could also
680 greatly benefit from the current increasing availability of forest inventory data to improve its
681 calibration using inverse modeling approaches (Hartig et al. 2012).

682

683 **Hypotheses, limitations and future directions to improve the model**

684 The high accuracy of ForCEEPS in predicting mean annual stand productivity of forests over a
685 few years thus opens great perspectives for ecological studies. However, this potential should

686 not conceal the simplifications and limits of our approach. Our results showed that explicitly
687 representing 2D-competition for light by considering crown size in the vertical canopy space
688 improved the accuracy of the predictions of short-term productivity compared to the ‘classic’
689 scheme of gap models (Bugmann 2001). Meanwhile, this novel development did not affect the
690 reliability of the model’s predictions of community composition and standing biomass in the
691 long term. Yet, introducing this change in the model implied to make some assumptions on
692 crown traits and foliage distribution in vertical space. There is an increasing number of studies
693 showing that these properties vary depending on species identity (Bayer et al. 2013, Forrester
694 and Albrecht 2014, Forrester et al. 2018), and the size and identity of neighboring trees (Poorter
695 et al. 2006, Williams et al. 2017, Niklaus et al. 2017). While future work may further improve
696 the representation of canopy space exploration by taking into account the plasticity of tree
697 architecture, we believe that the current version of the model relies on a sufficiently
698 parsimonious approach to explore new questions regarding above-ground tree-tree interactions
699 in mixed stands. Keeping track of tree coordinates in horizontal space - as already done in other
700 models (Bohn et al. 2014, Maréchaux and Chave 2017) - would allow to more finely tackle the
701 mechanism driving tree interactions, but this may come at the cost of losing the generality of
702 the model, as well as strongly increasing the simulation time.

703 We demonstrate in this study that both the climatic constraints and the variability in
704 species’ shade tolerances are crucial to predict short-term productivity with gap models. In
705 particular, we showed that differences in shade tolerance among species are key community
706 features driving diverse forest productivity, which has not been shown across such a wide
707 environmental gradient to our knowledge (Toïgo et al. 2018, Van de Peer et al. 2018). In turn,
708 this reinforces the need for further exploration of light-mediated tree interactions to understand
709 the mechanisms driving species assemblage and productivity in mixed forests. Although these
710 quantifications are necessarily related to the way the climatic growth-reducing factors and

711 competition for light are modelled, they nevertheless provide an *a posteriori* justification of the
712 processes embedded in these models. This also confirms the large potential of such models for
713 exploring how diversity affects forest functioning (Toïgo et al. 2018, Van de Peer et al. 2018,
714 Cordonnier et al. 2018a) and how climate change is mediating this effect (Morin et al. 2018).

715 Yet, this study considered short-term growth, i.e. tree or stand growth averaged across
716 a few years. Testing the performance of ForCEEPS on actual annual data of tree and stand
717 increments would have constituted an even stronger test. However, this kind of data is rarely
718 available for all trees on ~1000 m² plots (see Nehrbass-Ahles et al. 2014), especially for large
719 number of species and range of environmental conditions.

720 For the sake of generality, ForCEEPS relies on generic DBH-height relationships,
721 although DBH-height relationships are known to change with tree age and tree density (Trouvé
722 et al. 2015, Fortin et al. 2019). Improvements in this direction may be possible, even though
723 calibrating this allometric parameter would require more detailed inventory data (Rasche et al.
724 2012), and may have a very limited effect on the model's results when compared to the effect
725 of other parameters (see sensitivity analysis of the ForCLIM model by Morin et al. 2011 and
726 Huber et al. 2018).

727 More generally about long term predictions, reaching stronger robustness in predicting
728 long-term species coexistence and community composition would necessitate to better model
729 the occurrence of mortality events and regeneration. In fact, improving the representation of
730 these two processes is a main challenge in forest modelling, especially to better assess climate
731 change impacts on forest functioning (e.g. for mortality Bugmann et al. 2019, Cailleret et al.
732 2017, Hülsmann et al. 2018, Vanoni et al. 2019). Besides, although nutrients and water content
733 in the soil indirectly affects competition between trees (see Methods section), future
734 developments may lead to a multi-dimensional competition along several niche axes. One may
735 also notice that the results for the two Mediterranean sites presented here are already satisfying.

736 Furthermore, the impacts of abiotic (e.g., fire, extreme drought events) and biotic (e.g.,
737 pathogens, herbivory) disturbances are also key factors, that should be better considered by
738 these models in the future (Seidl et al. 2017).

739

740 **Mechanistic relevance of ForCEEPS parameters**

741 The analysis exploring the congruence between key ForCEEPS' parameters and
742 functional traits retrieved from the literature aimed at highlighting to what extent the parameters
743 describing species in ForCEEPS can be linked to their ecophysiology. First the negative
744 correlation between the growth parameter (g_S) and wood density appears meaningful as wood
745 density describes the carbon investment per unit volume of stem (Chaves et al 2009), thus
746 indicating that fast-growing species favored wood volume (i.e., space exploration) at the
747 expense of wood resistance to mechanical or biotic damages.

748 Shade tolerance is one of the features that segregates ecological groups of tree species
749 and that explain BEF patterns in forests. Some studies indicate that shade tolerance is related
750 to a combination of structural properties maximizing leaf area per unit of respiring biomass,
751 and to a combination of leaf properties optimizing photosynthesis per unit of nitrogen
752 investment. In particular shade-intolerant or pioneer species are frequently thought to display
753 higher light-saturated net photosynthesis (A_{max}) than shade-tolerant or late successional species
754 (Coste et al., 2005; Reich & Walters, 1994). Consistent with this later assertion, we found a
755 significant and consistent correlation between $ShTol_{seedlings}$ and A_{max} (Fig. 5), and to a lower
756 extent between $ShTol_S$ and A_{max} (Table S5). However no correlation was found with LMA ,
757 which echoes the debate regarding the multiple factors influencing this trait - including
758 ontogeny, leaf life span, and light environment - that can blur any expected pattern (Lusk &
759 Warton, 2007).

760 Drought tolerance (*DrTols*) is another key parameter that was positively correlated with
761 a number of functional traits (Table S5, Fig. 5). The best correlation, however, was found with
762 species embolism resistance (assessed through the water potential causing 50% loss of
763 conductivity, *P50*). This pattern is consistent with current ecophysiological knowledge that
764 xylem embolism is a key driver of species mortality during drought (Martin-StPaul et al 2017;
765 Adams et al 2018). Additionally, a significant but weaker correlation was found between *DrTols*
766 and the turgor loss point – a trait linked to the maintenance of leaf hydration and functions at
767 low water potential (Bartlett, Scoffoni, & Sack, 2012) and to stomatal control (Brodribb &
768 Holbrook, 2003; Martin-StPaul et al., 2017). This lower correlation is consistent with the fact
769 that the variability of turgor loss point is much more constrained among plants than the *P50*
770 (Martin-StPaul et al 2017). Interestingly, as for *Sh_tols*, *DrTols* was only weakly correlated with
771 wood density and *LMA*, which is probably related to their poor mechanistic relevance in the
772 species resistance to drought (Chave et al 2009 ; Bartlett et al 2012). Although performed on a
773 relatively small number of species, these results nevertheless pave the way for potential
774 improvement of the representation of drought tolerance in ForCEEPS, for instance by
775 implementing an hydraulic failure module that mechanistically integrate multiple traits (e.g.,
776 Martin-StPaul et al 2017). More generally, exploring the mechanistic relevance of gap model
777 parameters allows using functional trait databases to constrain them within realistic values and
778 avoid equifinalities issues.

779

780 **Research avenues for a new generation of forest gap models**

781 The large potential of forest dynamic models to tackle key questions in forest ecology has been
782 reviewed elsewhere (Ruiz-Benito et al. 2020), but we highlight that their role in providing more
783 robust predictions in response to global change components is increasingly emphasized

784 (McDowell 2020). Furthermore, we would like to focus on two related perspectives that are
785 arising from the validation at both short and long term shown here.

786

787 *Biodiversity and ecosystem functioning in forests*

788 The validation presented here opens perspectives for further tests of the effects of species
789 richness or functional diversity on forest productivity. Several attempts were conducted to use
790 gap models for studying diversity-productivity relationships (Morin et al. 2011, Bohn et al.
791 2017). Nevertheless, the models used had not been validated rigorously for monospecific
792 forests across such a wide range of species and environmental conditions, although the analyses
793 about the effect of diversity on ecosystem functioning strongly rely on the comparison with
794 monospecific stands (Loreau and Hector 2001, 2019). More precisely, the increased confidence
795 in the ability of gap models to simulate monospecific stands will improve their ability to test
796 non-additive effects in species mixtures (Gamfeldt and Roger 2017), i.e., effects directly related
797 to interspecific interactions. Furthermore, as ForCEEPS accurately predicts stand productivity
798 and long-term composition for the main species in Western Europe under a wide range of
799 conditions, we may expect a high robustness of the simulated BEF relationship.

800 Forest gap models simulate local interactions among trees, which have been reported as
801 fundamental drivers of mixture effects on forest functioning (Fichtner et al. 2018). Thus, the
802 simulated biodiversity patterns necessarily emerge from selection and complementarity effects
803 (Loreau and Hector 2001), the latter referring to niche differentiation processes among co-
804 existing species (as detailed in Morin et al. 2011) but also facilitative processes, depending on
805 the model structure. Niche differentiation processes notably include complementarity in
806 occupying canopy space (Jucker et al. 2015, Williams et al. 2017), and the 2-D crown
807 representation of ForCEEPS enables to better explore the way canopy packing occurs in
808 simulated mixtures and affects forest productivity. More generally, a growing body of evidence

809 suggests that structural diversity is a key driver of productivity in forests, independently of the
810 potential effects of other facets of diversity such as species richness and functional diversity
811 (Dănescu et al. 2016, Schnabel et al. 2019, Gough et al. 2019, Aponte et al. 2020). ForCEEPS
812 is a suitable tool to quantify the importance of these - often tangled - diversity facets across
813 large environmental gradients, with important consequence for our understating of BEF
814 relationships and for the management of diverse forests.

815 Furthermore, plasticity in crown size (or more precisely tree foliage area) may emerge
816 in the simulations due to species complementarity in light capture and/or response to
817 environmental fluctuations (e.g., climate). Intraspecific changes in crown architecture are
818 ultimately determined by changes in within-tree biomass allocation and branching patterns,
819 which have been shown to occur in mixed stands (Pretzsch 2014, Kunz et al. 2019, Guillemot
820 et al. 2020) but are not considered here. The modelling of such mixture effects is currently
821 hindered by data scarcity, and would probably necessitate implementing the spatial distribution
822 of the simulated trees in the horizontal space (Forrester et al. 2018).

823

824 *Testing coexistence mechanisms in the short and long term*

825 Species coexistence in forest gap models is based on two main mechanisms: first, trade-offs
826 arising from the life-history strategies such as high rates of colonization often being tied to low
827 shade tolerance, or a typically short lifespan of early successional, fast-growing trees; and
828 second, the fact that cyclical succession is occurring on each individual patch, so that species
829 with different properties are able to dominate during different parts of the cycle (Bazzaz 1979,
830 Rees et al. 2001). Exploring the relative importance of these mechanisms for allowing species
831 coexistence of simulated communities, but also for creating and maintaining diversity effects
832 on ecosystem functioning is a promising avenue for gap model applications (Falster et al. 2017,
833 Cordonnier et al. 2018b), especially if such an exploration is to be carried out across a large

834 range of conditions. This may ultimately lead to the formulation of new hypotheses, for instance
835 about the impact of climate change on species coexistence and forest functioning.

836 Finally, we also see further potential applications of models like ForCEEPS in the
837 design of forest policy. Large-scale forest restoration and reforestation programs are key to
838 prevent the most deleterious effects of climate change in the coming decade (Lewis et al. 2019).
839 Global initiatives such as the Bonn challenge are planning restoration at an unprecedented scale
840 (Verdone and Seidl 2017). Yet, we currently lack science-based guidelines for the design of
841 productive and resilient forest plantations in most environmental contexts. As mixed-species
842 plantations are thought to be a crucial nature-based solution for climate mitigation and
843 adaptation (Paquette et al. 2018), a generic and validated tool such as ForCEEPS can be used
844 to explore “management versus climate scenario” interactions and promote climate-smart
845 forestry at large scale. Thus, a new generation of forest gap models could foster the transfer of
846 BEF knowledge into forestry practice.

847 Generating new hypotheses from model outcomes is one of the main reasons of using
848 models in ecology in the first place, together with the support they may provide for better
849 understanding the systems and processes at play, and their ability to yield predictions across
850 spatial and temporal scales (Levins 1966). As they did for more than 50 years, we believe that
851 gap models in general, and the ForCEEPS model presented here in particular, maintain a key
852 role for these purposes in forest ecology and management. More generally, because they seek
853 for generality while aiming at relying on functional processes, such models are likely to be
854 highly relevant to provide robust predictions of ecosystem composition, structure and
855 functioning in a context of very uncertain future for forests (McDowell et al. 2020).

856

857

858

859 **References**

- 860 Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T.
861 Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z.
862 Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N.
863 Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals
864 emerging climate change risks for forests. *Forest Ecology and Management* 259:660–
865 684.
- 866 Aponte, C., S. Kasel, C. R. Nitschke, M. A. Tanase, H. Vickers, L. Parker, M. Fedrigo, M.
867 Kohout, P. Ruiz-Benito, M. A. Zavala, and L. T. Bennett. 2020. Structural diversity
868 underpins carbon storage in Australian temperate forests. *Global Ecology and*
869 *Biogeography*:geb.13038.
- 870 Bartlett, M. K., Scoffoni, C., and Sack, L. 2012. The determinants of leaf turgor loss point and
871 prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology*
872 *Letters*, 15:393–405. doi: 10.1111/j.1461-0248.2012.01751.x
- 873 Bayer, D., S. Seifert, and H. Pretzsch. 2013. Structural crown properties of Norway spruce
874 (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in mixed versus pure
875 stands revealed by terrestrial laser scanning. *Trees-Structure and Function* 27:1035–
876 1047.
- 877 Bazzaz, F. A. 1979. Physiological Ecology of Plant Succession. *Annual Review of Ecology*
878 *and Systematics* 10:351–371.
- 879 Bohn, F. J., K. Frank, and A. Huth. 2014. Of climate and its resulting tree growth: Simulating
880 the productivity of temperate forests. *Ecological Modelling* 278:9–17.
- 881 Bohn, F. J., and A. Huth. 2017. The importance of forest structure to biodiversity–
882 productivity relationships. *Royal Society Open Science* 4:160521
- 883 Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest

884 productivity – evidence since the middle of the 20th century. *Global Change Biology*
885 12:862–882.

886 Brodrigg, T. J., and Holbrook, N. M. 2003. Stomatal closure during leaf dehydration,
887 correlation with other leaf physiological traits. *Plant Physiology*, 132:2166–2173. doi:
888 10.1104/pp.103.023879

889 Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a
890 computer model of forest growth. *Journal of Ecology* 60:849–872.

891 Bugmann, H. 1994. On the Ecology of mountainous forests in a changing climate: A
892 simulation study. Eidgenössische Technische Hochschule, Zürich.

893 Bugmann, H. 1996. A simplified forest model to study species composition along climate
894 gradients. *Ecology* 77:2055–2074.

895 Bugmann, H. 2001. A review of forest gap models. *Climatic Change* 51:259–305.

896 Bugmann, H., R. Seidl, F. Hartig, F. Bohn, J. Brūna, M. Cailleret, L. François, J. Heinke, A.-
897 J. Henrot, T. Hickler, L. Hülsmann, A. Huth, I. Jacquemin, C. Kollas, P. Lasch-Born, M.
898 J. Lexer, J. Merganič, K. Merganičová, T. Mette, B. R. Miranda, D. Nadal-Sala, W.
899 Rammer, A. Rammig, B. Reineking, E. Roedig, S. Sabaté, J. Steinkamp, F. Suckow, G.
900 Vacchiano, J. Wild, C. Xu, and C. P. O. Reyer. 2019. Tree mortality submodels drive
901 simulated long-term forest dynamics: assessing 15 models from the stand to global scale.
902 *Ecosphere* 10:e02616.

903 Bugmann, H., and A. M. Solomon. 2000. Explaining forest composition and biomass across
904 multiple biogeographical regions. *Ecological Applications* 10:95–114.

905 Cailleret, M., S. Jansen, E. M. R. Robert, L. Desoto, T. Aakala, J. A. Antos, B. Beikircher, C.
906 Bigler, H. Bugmann, M. Caccianiga, V. Čada, J. J. Camarero, P. Cherubini, H. Cochard,
907 M. R. Coyea, K. Čufar, A. J. Das, H. Davi, S. Delzon, M. Dorman, G. Gea-Izquierdo, S.
908 Gillner, L. J. Haavik, H. Hartmann, A. Hereş, K. R. Hultine, P. Janda, J. M. Kane, V. I.

909 Kharuk, T. Kitzberger, T. Klein, K. Kramer, F. Lens, T. Levanic, J. C. Linares Calderon,
910 F. Lloret, R. Lobo-Do-Vale, F. Lombardi, R. López Rodríguez, H. Mäkinen, S. Mayr, I.
911 Mészáros, J. M. Metsaranta, F. Minunno, W. Oberhuber, A. Papadopoulos, M.
912 Peltoniemi, A. M. Petritan, B. Rohner, G. Sangüesa-Barreda, D. Sarris, J. M. Smith, A.
913 B. Stan, F. Sterck, D. B. Stojanović, M. L. Suarez, M. Svoboda, R. Tognetti, J. M.
914 Torres-Ruiz, V. Trotsiuk, R. Villalba, F. Vodde, A. R. Westwood, P. H. Wyckoff, N.
915 Zafirov, and J. Martínez-Vilalta. 2017. A synthesis of radial growth patterns preceding
916 tree mortality. *Global Change Biology* 23:1675–1690.

917 Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and
918 consequences of resource heterogeneity in forests: Interspecific variation in light
919 transmission by canopy trees. *Canadian Journal of Forest Research* 24:337–349.

920 Castagneyrol, B., B. Giffard, C. Péré, and H. Jactel. 2013. Plant apparency, an overlooked
921 driver of associational resistance to insect herbivory. *Journal of Ecology* 101:418–429.

922 Chapin, F. S., J. T. Randerson, A. D. McGuire, J. A. Foley, and C. B. Field. 2008. Changing
923 feedbacks in the climate-biosphere system. *Frontiers in Ecology and the Environment*
924 6:313–320.

925 Charru, M., I. Seynave, F. Morneau, and J.-D. Bontemps. 2010. Recent changes in forest
926 productivity: An analysis of national forest inventory data for common beech (*Fagus*
927 *sylvatica* L.) in north-eastern France. *Forest Ecology and Management* 260:864–874.

928 Chauvet, M., G. Kunstler, J. Roy, and X. Morin. 2017. Using a forest dynamics model to link
929 community assembly processes and traits structure. *Functional Ecology* in press.

930 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E. 2009.
931 Towards a worldwide wood economics spectrum. *Ecology Letters*, 12:351–366. doi:
932 10.1111/j.1461-0248.2009.01285.x

933 Coomes, D. A., O. Flores, R. Holdaway, T. Jucker, E. R. Lines, and M. C. Vanderwel. 2014.

934 Wood production response to climate change will depend critically on forest
935 composition and structure. *Global Change Biology* 20:3632–3645.

936 Cordonnier, T., T. Bourdier, G. Kunstler, C. Piedallu, and B. Courbaud. 2018a. Covariation
937 between tree size and shade tolerance modulates mixed-forest productivity. *Annals of*
938 *Forest Science* 75:101.

939 Cordonnier, T., G. Kunstler, B. Courbaud, and X. Morin. 2018b. Managing tree species
940 diversity and ecosystem functioning through coexistence mechanisms. *Annals of Forest*
941 *Sciences*.

942 Cordonnier, T., C. Smadi, G. Kunstler, and B. Courbaud. 2019. Asymmetric competition,
943 ontogenetic growth and size inequality drive the difference in productivity between two-
944 strata and one-stratum forest stands. *Theoretical Population Biology*.

945 Coste, S., Roggy, J. C., Imbert, P., Born, C., Bonal, D., and Dreyer, E. 2005. Leaf
946 photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen
947 concentration and shade tolerance. *Tree Physiology*, 25:1127–1137. doi:
948 10.1093/treephys/25.9.1127

949 Dănescu, A., A. T. Albrecht, and J. Bauhus. 2016. Structural diversity promotes productivity
950 of mixed, uneven-aged forests in southwestern Germany. *Oecologia* 182:319–333.

951 DeSoto, L., M. Cailleret, F. Sterck, S. Jansen, K. Kramer, E. M. R. Robert, T. Aakala, M. M.
952 Amoroso, C. Bigler, J. J. Camarero, K. Čufar, G. Gea-Izquierdo, S. Gillner, L. J. Haavik,
953 A. M. Hereş, J. M. Kane, V. I. Kharuk, T. Kitzberger, T. Klein, T. Levanič, J. C. Linares,
954 H. Mäkinen, W. Oberhuber, A. Papadopoulos, B. Rohner, G. Sangüesa-Barreda, D. B.
955 Stojanovic, M. L. Suárez, R. Villalba, and J. Martínez-Vilalta. 2020. Low growth
956 resilience to drought is related to future mortality risk in trees. *Nature Communications*
957 11:1–9.

958 Didion, M., A. D. Kupferschmid, A. Wolf, and H. Bugmann. 2011. Ungulate herbivory

959 modifies the effects of climate change on mountain forests. *Climatic Change* 109:647–
960 669.

961 Didion, M., A. D. Kupferschmid, A. Zingg, L. Fahse, and H. Bugmann. 2009. Gaining local
962 accuracy while not losing generality — extending the range of gap model applications.
963 *Canadian Journal of Forest Research* 39:1092–1107.

964 Dobbertin, M. 2005. Tree growth as indicator of tree vitality and of tree reaction to
965 environmental stress: a review. *European Journal of Forest Research* 124:319–333.

966 Dufrêne, E., H. Davi, C. François, G. le Maire, V. Le Dantec, and A. Granier. 2005.
967 Modelling carbon and water cycles in a beech forest: Part I: Model description and
968 uncertainty analysis on modelled NEE. *Ecological Modelling* 185:407–436.

969 Eermak, J. 1998. Leaf distribution in large trees and stands of the floodplain forest in southern
970 Moravia. *Tree Physiology* 18:727–737.

971 Ellenberg, H., and D. Mueller-Dombois. 1966. Tentative physiognomic-ecological
972 classification of plant formations of the Earth. *Ber. Geobot. Inst. ETH* 37:21–55

973 Esquivel-Muelbert, A., T. R. Baker, K. G. Dexter, S. L. Lewis, R. J. W. Brienen, T. R.
974 Feldpausch, J. Lloyd, A. Monteagudo-Mendoza, L. Arroyo, E. Álvarez-Dávila, N.
975 Higuchi, B. S. Marimon, B. H. Marimon-Junior, M. Silveira, E. Vilanova, E. Gloor, Y.
976 Malhi, J. Chave, J. Barlow, D. Bonal, N. Davila Cardozo, T. Erwin, S. Fauset, B.
977 Hérault, S. Laurance, L. Poorter, L. Qie, C. Stahl, M. J. P. Sullivan, H. ter Steege, V. A.
978 Vos, P. A. Zuidema, E. Almeida, E. Almeida de Oliveira, A. Andrade, S. A. Vieira, L.
979 Aragão, A. Araujo-Murakami, E. Arets, G. A. Aymard C, C. Baraloto, P. B. Camargo, J.
980 G. Barroso, F. Bongers, R. Boot, J. L. Camargo, W. Castro, V. Chama Moscoso, J.
981 Comiskey, F. Cornejo Valverde, A. C. Lola da Costa, J. del Aguila Pasquel, A. Di Fiore,
982 L. Fernanda Duque, F. Elias, J. Engel, G. Flores Llampazo, D. Galbraith, R. Herrera
983 Fernández, E. Honorio Coronado, W. Hubau, E. Jimenez-Rojas, A. J. N. Lima, R. K.

984 Umetsu, W. Laurance, G. Lopez-Gonzalez, T. Lovejoy, O. Aurelio Melo Cruz, P. S.
 985 Morandi, D. Neill, P. Núñez Vargas, N. C. Pallqui Camacho, A. Parada Gutierrez, G.
 986 Pardo, J. Peacock, M. Peña-Claros, M. C. Peñuela-Mora, P. Petronelli, G. C. Pickavance,
 987 N. Pitman, A. Prieto, C. Quesada, H. Ramírez-Angulo, M. Réjou-Méchain, Z. Restrepo
 988 Correa, A. Roopsind, A. Rudas, R. Salomão, N. Silva, J. Silva Espejo, J. Singh, J.
 989 Stropp, J. Terborgh, R. Thomas, M. Toledo, A. Torres-Lezama, L. Valenzuela Gamarra,
 990 P. J. van de Meer, G. van der Heijden, P. van der Hout, R. Vasquez Martinez, C. Vela, I.
 991 C. G. Vieira, and O. L. Phillips. 2019. Compositional response of Amazon forests to
 992 climate change. *Global Change Biology* 25:39–56.

993 Falster, D. S., Å. Brännström, M. Westoby, and U. Dieckmann. 2017. Multitrait successional
 994 forest dynamics enable diverse competitive coexistence. *Proceedings of the National*
 995 *Academy of Sciences of the United States of America* 114:E2719–E2728.

996 Falster, D. S., Duursma, R. A., and FitzJohn, R. G. 2018. How functional traits influence
 997 plant growth and shade tolerance across the life cycle. *Proceedings of the National*
 998 *Academy of Sciences* 115: E6789-E6798.

999 Fichtner, A., W. Härdtle, H. Bruelheide, M. Kunz, Y. Li, and Goddert Von Oheimb. 2018.
 1000 Neighbourhood interactions driveoveryielding in mixed-species tree communities.
 1001 *Nature Communications* 9:1144.

1002 Forrester, D. I., and A. T. Albrecht. 2014. Light absorption and light-use efficiency in
 1003 mixtures of *Abies alba* and *Picea abies* along a productivity gradient. *Forest Ecology and*
 1004 *Management* 328:94–102.

1005 Forrester, D. I., C. Ammer, P. J. Annighöfer, I. Barbeito, K. Bielak, A. Bravo-Oviedo, L.
 1006 Coll, M. del Río, L. Drössler, M. Heym, V. Hurt, M. Löf, J. den Ouden, M. Pach, M. G.
 1007 Pereira, B. N. E. Plaga, Q. Ponette, J. Skrzyszewski, H. Sterba, M. Svoboda, T. M.
 1008 Zlatanov, and H. Pretzsch. 2018. Effects of crown architecture and stand structure on

1009 light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests
1010 along a productivity and climate gradient through Europe. *Journal of Ecology* 106:746–
1011 760.

1012 Fortin, M., R. Van Couwenberghe, V. Perez, and C. Piedallu. 2019. Evidence of climate
1013 effects on the height-diameter relationships of tree species. *Annals of Forest Science*
1014 76:1.

1015 Fyllas, N. M., E. Gloor, L. M. Mercado, S. Sitch, C. A. Quesada, T. F. Domingues, D. R.
1016 Galbraith, A. Torre-Lezama, E. Vilanova, H. Ramírez-Angulo, N. Higuchi, D. A. Neill,
1017 M. Silveira, L. Ferreira, G. A. Aymard C., Y. Malhi, O. L. Phillips, and J. Lloyd. 2014.
1018 Analysing Amazonian forest productivity using a new individual and trait-based model
1019 (TFS v.1). *Geoscientific Model Development* 7:1251–1269.

1020 Gamfeldt, L., and F. Roger. 2017, June 22. Revisiting the biodiversity-ecosystem
1021 multifunctionality relationship. Nature Publishing Group.

1022 Gough, C. M., J. W. Atkins, R. T. Fahey, and B. S. Hardiman. 2019. High rates of primary
1023 production in structurally complex forests. *Ecology* 100.

1024 Guillemot, J., M. Kunz, F. Schnabel, A. Fichtner, C. P. Madsen, T. Gebauer, W. Härdtle, G.
1025 von Oheimb, and C. Potvin. 2020. Neighbourhood-mediated shifts in tree biomass
1026 allocation drive overyielding in tropical species mixtures. *New Phytologist*:nph.16722.

1027 Guillemot, J., C. Francois, G. Hmimina, E. Dufrêne, N. K. Martin-StPaul, K. Soudani, G.
1028 Marie, J.-M. Ourcival, and N. Delpierre. 2017. Environmental control of carbon
1029 allocation matters for modelling forest growth. *New Phytologist* 214:180–193.

1030 Hardiman, B. S., G. Bohrer, C. M. Gough, C. S. Vogel, and P. S. Curtis. 2011. The role of
1031 canopy structural complexity in wood net primary production of a maturing northern
1032 deciduous forest. *Ecology* 92:1818–1827.

1033 Hartig, F., J. Dyke, T. Hickler, S. I. Higgins, R. B. O’Hara, S. Scheiter, and A. Huth. 2012.

- 1034 Connecting dynamic vegetation models to data - an inverse perspective. *Journal of*
1035 *Biogeography* 39:2240–2252.
- 1036 Huber, N., H. Bugmann, and V. Lafond. 2018. Global sensitivity analysis of a dynamic
1037 vegetation model: Model sensitivity depends on successional time, climate and
1038 competitive interactions. *Ecological Modelling* 368:377–390.
- 1039 Hülsmann, L., H. Bugmann, M. Cailleret, and P. Brang. 2018. How to kill a tree: empirical
1040 mortality models for 18 species and their performance in a dynamic forest model.
1041 *Ecological Applications* 28:522–540.
- 1042 IFN. 2016. Les Résultats Issus des Campagnes d’Inventaire entre 2011 et 2016. Nogent-sur-
1043 Vernisson.
- 1044 IGN. 2018. Données brutes de l’Inventaire forestier national. [https://inventaire-](https://inventaire-forestier.ign.fr/spip.php?rubrique159)
1045 [forestier.ign.fr/spip.php?rubrique159](https://inventaire-forestier.ign.fr/spip.php?rubrique159).
- 1046 Jactel, H., E. S. Gritti, L. Drössler, D. I. Forrester, W. L. Mason, X. Morin, H. Pretzsch, and
1047 B. Castagneyrol. 2018. Positive biodiversity-productivity relationships in forests: climate
1048 matters. *Biology Letters* 14:1–4.
- 1049 Jourdan, M., G. Kunstler, and X. Morin. 2019a. How neighbourhood interactions control the
1050 temporal stability and resilience to drought of trees in mountain forests. *Journal of*
1051 *Ecology*:1365-2745.13294.
- 1052 Jourdan, M., F. Lebourgeois, and X. Morin. 2019b. The effect of tree diversity on the
1053 resistance and recovery of forest stands in the French Alps may depend on species
1054 differences in hydraulic features. *Forest Ecology and Management* 450:117486.
- 1055 Jucker, T., D. Avăcăriței, I. Bărnoaiea, G. Duduman, O. Bouriaud, and D. A. Coomes. 2016.
1056 Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology*
1057 104:388–398.
- 1058 Jucker, T., O. Bouriaud, and D. A. Coomes. 2015. Crown plasticity enables trees to optimize

1059 canopy packing in mixed-species forests. *Functional Ecology* 29.

1060 Kattge, J., S. Diaz, S. Lavorel, C. Prentice, P. Leadley, G. Bonisch, E. Garnier, M. Westoby,
1061 P. B. Reich, I. J. Wright, J. H. C. Cornelissen, C. Violle, S. P. Harrison, P. M. van
1062 Bodegom, M. Reichstein, B. J. Enquist, N. A. Soudzilovskaia, D. D. Ackerly, M. Anand,
1063 O. Atkin, M. Bahn, T. R. Baker, D. Baldocchi, R. Bekker, C. C. Blanco, B. Blonder, W.
1064 J. Bond, R. Bradstock, D. E. Bunker, F. Casanoves, J. Cavender-Bares, J. Q. Chambers,
1065 F. S. Chapin, J. Chave, D. Coomes, W. K. Cornwell, J. M. Craine, B. H. Dobrin, L.
1066 Duarte, W. Durka, J. Elser, G. Esser, M. Estiarte, W. F. Fagan, J. Fang, F. Fernandez-
1067 Mendez, A. Fidelis, B. Finegan, O. Flores, H. Ford, D. Frank, G. T. Freschet, N. M.
1068 Fyllas, R. V. Gallagher, W. A. Green, A. G. Gutierrez, T. Hickler, S. I. Higgins, J. G.
1069 Hodgson, A. Jalili, S. Jansen, C. A. Joly, A. J. Kerkhoff, D. Kirkup, K. Kitajima, M.
1070 Kleyer, S. Klotz, J. M. H. Knops, K. Kramer, I. Kuhn, H. Kurokawa, D. Laughlin, T. D.
1071 Lee, M. Leishman, F. Lens, T. Lenz, S. L. Lewis, J. Lloyd, J. Llusia, F. Louault, S. Ma,
1072 M. D. Mahecha, P. Manning, T. Massad, B. E. Medlyn, J. Messier, A. T. Moles, S. C.
1073 Muller, K. Nadrowski, S. Naeem, U. Niinemets, S. Nollert, A. Nuske, R. Ogaya, J.
1074 Oleksyn, V. G. Onipchenko, Y. Onoda, J. Ordonez, G. Overbeck, W. A. Ozinga, S.
1075 Patino, S. Paula, J. G. Pausas, J. Penuelas, O. L. Phillips, V. Pillar, H. Poorter, L.
1076 Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B. Reu, L. Sack,
1077 B. Salgado-Negre, J. Sardans, S. Shiodera, B. Shipley, A. Siefert, E. Sosinski, J. F.
1078 Soussana, E. Swaine, N. Swenson, K. Thompson, P. Thornton, M. Waldram, E. Weiher,
1079 M. White, S. White, S. J. Wright, B. Yguel, S. Zaehle, A. E. Zanne, and C. Wirth. 2011.
1080 TRY - a global database of plant traits. *Global Change Biology* 17:2905–2935.

1081 Keenan, T. F., and Niinemets, Ü. 2016. Global leaf trait estimates biased due to plasticity in
1082 the shade. *Nature Plants*, 3:1–6. doi: 10.1038/nplants.2016.201

1083 Korner, C., R. Asshoff, O. Bignucolo, S. Hättenschwiler, S. G. Keel, S. Peláez-Riedl, S.

1084 Pepin, R. T. W. Siegwolf, and G. Zotz. 2005. Carbon flux and growth in mature
1085 deciduous forest trees exposed to elevated CO₂. *Science* 309:1360–1362.

1086 Kunz, M., A. Fichtner, W. Härdtle, P. Raunonen, H. Bruelheide, and G. von Oheimb. 2019,
1087 December 1. Neighbour species richness and local structural variability modulate
1088 aboveground allocation patterns and crown morphology of individual trees. Blackwell
1089 Publishing Ltd.

1090 Levins, R. 1966. The strategy of model building in population ecology. *American Scientist*
1091 54:421–451.

1092 Lewis, S. L., C. E. Wheeler, E. T. A. Mitchard, and A. Koch. 2019. Restoring natural forests
1093 is the best way to remove atmospheric carbon. *Nature* 568:25–28.

1094 Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D.
1095 McGuire, F. Bozzato, H. Pretzsch, S. de-Miguel, A. Paquette, B. Hérault, M. Scherer-
1096 Lorenzen, C. B. Barrett, H. B. Glick, G. M. Hengeveld, G.-J. Nabuurs, S. Pfautsch, H.
1097 Viana, A. C. Vibrans, C. Ammer, P. Schall, D. Verbyla, N. Tchebakova, M. Fischer, J. V
1098 Watson, H. Y. H. Chen, X. Lei, M.-J. Schelhaas, H. Lu, D. Gianelle, E. I. Parfenova, C.
1099 Salas, E. Lee, B. Lee, H. S. Kim, H. Bruelheide, D. A. Coomes, D. Piotta, T.
1100 Sunderland, B. Schmid, S. Gourlet-Fleury, B. Sonké, R. Tavani, J. Zhu, S. Brandl, J.
1101 Vayreda, F. Kitahara, E. B. Searle, V. J. Neldner, M. R. Ngugi, C. Baraloto, L. Frizzera,
1102 R. Bałazy, J. Oleksyn, T. Zawila-Niedźwiecki, O. Bouriaud, F. Bussotti, L. Finér, B.
1103 Jaroszewicz, T. Jucker, F. Valladares, A. M. Jagodzinski, P. L. Peri, C. Gonmadje, W.
1104 Marthy, T. O’Brien, E. H. Martin, A. R. Marshall, F. Rovero, R. Bitariho, P. A. Niklaus,
1105 P. Alvarez-Loayza, N. Chamuya, R. Valencia, F. Mortier, V. Wortel, N. L. Engone-
1106 Obiang, L. V Ferreira, D. E. Odeke, R. M. Vasquez, S. L. Lewis, and P. B. Reich. 2016.
1107 Positive biodiversity-productivity relationship predominant in global forests. *Science*
1108 354.

- 1109 Limousin, J. M., S. Rambal, J. M. Ourcival, A. Rocheteau, R. Joffre, and R. Rodriguez-
1110 Cortina. 2009. Long-term transpiration change with rainfall decline in a Mediterranean
1111 *Quercus ilex* forest. *Global Change Biology* 15:2163–2175.
- 1112 Lindner, M., M. Maroschek, S. Netherer, A. Kremer, A. Barbati, J. Garcia-Gonzalo, R. Seidl,
1113 S. Delzon, P. Corona, M. Kolström, M. J. Lexer, and M. Marchetti. 2010. Climate
1114 change impacts, adaptive capacity, and vulnerability of European forest ecosystems.
1115 *Forest Ecology and Management* 259:698–709.
- 1116 Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity
1117 experiments. *Nature* 412:72–76.
- 1118 Loreau, M., and A. Hector. 2019. Not even wrong: Comment by Loreau and Hector. *Ecology*.
- 1119 Lusk, C. H., and Warton, D. I. 2007. Global meta-analysis shows that relationships of leaf
1120 mass per area with species shade tolerance depend on leaf habit and ontogeny. *New*
1121 *Phytologist*, 176:764–774. doi: 10.1111/j.1469-8137.2007.02264.x
- 1122 Makela, A., J. Landsberg, A. R. Ek, T. E. Burk, M. Ter-Mikaelian, G. I. Agren, C. D. Oliver,
1123 and P. Puttonen. 2000. Process-based models for forest ecosystem management: current
1124 state of the art and challenges for practical implementation. *Tree Physiology* 20:289–
1125 298.
- 1126 Maréchaux, I., and J. Chave. 2017. An individual-based forest model to jointly simulate
1127 carbon and tree diversity in Amazonia: description and applications. *Ecological*
1128 *Monographs* 87:632–664.
- 1129 Martin-StPaul, N., S. Delzon, and H. Cochard. 2017. Plant resistance to drought depends on
1130 timely stomatal closure. *Ecology Letters* 20:1437–1447. doi: 10.1111/ele.12851
- 1131 McDowell, N. G., C. D. Allen, K. Anderson-Teixeira, B. H. Aukema, B. Bond-Lamberty, L.
1132 Chini, J. S. Clark, M. Dietze, C. Grossiord, A. Hanbury-Brown, G. C. Hurtt, R. B.
1133 Jackson, D. J. Johnson, L. Kueppers, J. W. Lichstein, K. Ogle, B. Poulter, T. A. M.

- 1134 Pugh, R. Seidl, M. G. Turner, M. Uriarte, A. P. Walker, and C. Xu. 2020. Pervasive
1135 shifts in forest dynamics in a changing world. *Science* 368:eaaz9463.
- 1136 Mette, T., A. Albrecht, C. Ammer, P. Biber, U. Kohnle, and H. Pretzsch. 2009. Evaluation of
1137 the forest growth simulator SILVA on dominant trees in mature mixed Silver fir–
1138 Norway spruce stands in South-West Germany. *Ecological Modelling* 220:1670–1680.
- 1139 Mina, M., H. Bugmann, T. Cordonnier, F. Irauschek, M. Klopčič, M. Pardos, and M.
1140 Cailleret. 2017. Future ecosystem services from European mountain forests under
1141 climate change. *Journal of Applied Ecology* 54:389–401.
- 1142 Mitscherlich, G., and K. von Gadow. 1968. Über den Zuwachsverlust bei der Ästung von
1143 Nadelbäumen. *Allgemeine Forst- und Jagdzeitung*.
- 1144 Moore, A. D. 1989. On the maximum growth equation used in forest gap simulation models.
1145 *Ecological Modelling* 45:63–67.
- 1146 Morin, X., L. Fahse, H. Jactel, M. Scherer-Lorenzen, R. García-Valdés, and H. Bugmann.
1147 2018. Long-term response of forest productivity to climate change is mostly driven by
1148 change in tree species composition. *Scientific Reports* 8:5627.
- 1149 Morin, X., L. Fahse, M. Scherer-Lorenzen, and H. Bugmann. 2011. Tree species richness
1150 promotes productivity in temperate forests through strong complementarity between
1151 species. *Ecology Letters* 14:1211–1219.
- 1152 Nadrowski, K., C. Wirth, and M. Scherer-Lorenzen. 2010. Is forest diversity driving
1153 ecosystem function and service? *Current Opinion in Environmental Sustainability* 2:75–
1154 79.
- 1155 Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., ... , and
1156 Frank, D. 2014. The influence of sampling design on tree-ring-based quantification of
1157 forest growth. *Global Change Biology* 20:2867-2885.
- 1158 Niklaus, P. A., M. Baruffol, J.-S. He, K. Ma, and B. Schmid. 2017. Can niche plasticity

1159 promote biodiversity-productivity relationships through increased complementarity?
1160 Ecology 98:1104–1116.

1161 Niinemets, U., and F. Valladares. 2006. Tolerance to shade, drought and waterlogging of
1162 temperate, Northern hemisphere trees and shrubs. *Ecological Monographs* 76:521–547.

1163 Norby, R. J., and D. R. Zak. 2011. Ecological Lessons from Free-Air CO₂ Enrichment
1164 (FACE) Experiments. *Annual Review of Ecology, Evolution, and Systematics* 42:181–
1165 203.

1166 Pacala, S. W., C. D. Canham, and J. A. Silander. 1993. Forest Models Defined by Field-
1167 Measurements .1. the Design of a Northeastern Forest Simulator. *Canadian Journal of*
1168 *Forest Research-Revue Canadienne De Recherche Forestiere* 23:1980–1988.

1169 Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A.
1170 Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D.
1171 McGuire, S. Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A large and persistent
1172 carbon sink in the world’s forests. *Science (New York, N.Y.)* 333:988–93.

1173 Paquette, A., A. Hector, B. Castagneyrol, M. Vanhellefont, J. Koricheva, M. Scherer-
1174 Lorenzen, and K. Verheyen. 2018. A million and more trees for science. *Nature Ecology*
1175 *& Evolution* 2:763–766.

1176 Van de Peer, T., K. Verheyen, Q. Ponette, N. N. Setiawan, and B. Muys. 2018. Overyielding
1177 in young tree plantations is driven by local complementarity and selection effects related
1178 to shade tolerance. *Journal of Ecology* 106:1096–1105.

1179 Van Pelt, R., S. C. Sillett, W. A. Kruse, J. A. Freund, and R. D. Kramer. 2016. Emergent
1180 crowns and light-use complementarity lead to global maximum biomass and leaf area in
1181 *Sequoia sempervirens* forests. *Forest Ecology and Management* 375:279–308.

1182 Pfister, C., and H. Bugmann. 2000. Impacts of interannual climate variability on past and
1183 future forest composition. *Regional Environmental Change* 1:112–125.

- 1184 Poorter, L., L. Bongers, and F. Bongers. 2006. Architecture of 54 moist-forest tree species:
1185 traits, trade-offs, and functional groups. *Ecology* 87:1289-1301.
- 1186 Pretzsch, H. 2014. Canopy space filling and tree crown morphology in mixed-species stands
1187 compared with monocultures. *Forest Ecology and Management* 327:251–264.
- 1188 Pretzsch, H., D. I. Forrester, and T. Rötzer. 2015. Representation of species mixing in forest
1189 growth models. A review and perspective. *Ecological Modelling* 313:276–292.
- 1190 Purves, D. W., J. W. Lichstein, N. Strigul, and S. W. Pacala. 2008. Predicting and
1191 understanding forest dynamics using a simple tractable model. *Proceedings of the*
1192 *National Academy of Science of the U.S.A* 105:17018–17022.
- 1193 R-Core-Team. 2018. R: A language and environment for statistical computing. R Foundation
1194 for Statistical Computing, Vienna, Austria.
- 1195 Rambal, S., M. Lempereur, J. M. Limousin, N. K. Martin-StPaul, J. M. Ourcival, and J.
1196 Rodríguez-Calcerrada. 2014. How drought severity constrains gross primary
1197 production(GPP) and its partitioning among carbon pools in a *Quercus ilex* coppice?
1198 *Biogeosciences* 11:6855–6869.
- 1199 Rameau, J.-C., D. Mansion, and G. Dumé. 1989. Flore forestière française. Guide écologique
1200 illustré. 1. Plaines et collines. Institut pour la Développement Forestier, Ministère de
1201 l’Agriculture et de la forêt, Paris.
- 1202 Rameau, J.-C., D. Mansion, G. Dumé, and C. Gauberville. 2008. Flore forestière française.
1203 Guide écologique illustré. 3. Région Méditerranéenne. Institut pour la Développement
1204 Forestier, Paris.
- 1205 Rasche, L., L. Fahse, A. Zingg, and H. Bugmann. 2011. Getting a virtual forester fit for the
1206 challenge of climatic change. *Journal of Applied Ecology* 48:1174–1186.
- 1207 Rasche, L., L. Fahse, A. Zingg, and H. Bugmann. 2012. Enhancing gap model accuracy by
1208 modeling dynamic height growth and dynamic maximum tree height. *Ecological*

1209 Modelling 232:133–143.

1210 Rees, M., R. Condit, M. Crawley, S. Pacala, and D. Tilman. 2001. Long-term studies of
1211 vegetation dynamics. *Science* 293:650–655.

1212 Reich, P. B. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto.
1213 *Journal of Ecology* 102: 275–301. doi: 10.1111/1365-2745.12211

1214 Reich, P. B., and Walters, M. B. 1994. Photosynthesis-nitrogen relations in Amazonian tree
1215 species. *Oecologia* 97(1), 73–81. doi: 10.1007/BF00317910

1216 del Río, M., H. Pretzsch, R. Ruíz-Peinado, E. Ampoorter, P. Annighöfer, I. Barbeito, K.
1217 Bielak, G. Brazaitis, L. Coll, L. Drössler, M. Fabrika, D. I. Forrester, M. Heym, V. Hurt,
1218 V. Kurylyak, M. Löf, F. Lombardi, E. Madrickiene, B. Matović, F. Mohren, R. Motta, J.
1219 den Ouden, M. Pach, Q. Ponette, G. Schütze, J. Skrzyszewski, V. Sramek, H. Sterba, D.
1220 Stojanović, M. Svoboda, T. M. Zlatanov, and A. Bravo-Oviedo. 2017. Species
1221 interactions increase the temporal stability of community productivity in *Pinus*
1222 *sylvestris-Fagus sylvatica* mixtures across Europe. *Journal of Ecology* 105:1032–1043.

1223 Ruiz-Benito, P., G. Vacchiano, E. R. Lines, C. P. O. Reyer, S. Ratcliffe, X. Morin, F. Hartig,
1224 A. Mäkelä, R. Yousefpour, J. E. Chaves, A. Palacios-Orueta, M. Benito-Garzón, C.
1225 Morales-Molino, J. J. Camarero, A. S. Jump, J. Kattge, A. Lehtonen, A. Ibrom, H. J. F.
1226 Owen, and M. A. Zavala. 2020. Available and missing data to model impact of climate
1227 change on European forests. *Ecological Modelling* 416:108870.

1228 San-Miguel-Ayanz, J., de Rigo, D., Caudullo G., Houston Durrant, T., Mauri, A., Tinner, W.,
1229 Ballian, D., Beck, P., Birks, H. J. B., Eaton, E., Enescu, C. M., Pasta, S., Popescu, I.,
1230 Ravazzi, C., Welk, E., Abad Viñas, R., Azevedo, J. C., Barbati, A., Barre, B. 2016.
1231 European Atlas of Forest Tree Species. Page (A. San-Miguel-Ayanz, J., de Rigo, D.,
1232 Caudullo, G., Houston Durrant, T., Mauri, Ed.). European Commission, Luxembourg.

1233 Schnabel, F., J. A. Schwarz, A. Dănescu, A. Fichtner, C. A. Nock, J. Bauhus, and C. Potvin.

1234 2019. Drivers of productivity and its temporal stability in a tropical tree diversity
1235 experiment. *Global Change Biology* 25: 4257-4272

1236 Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry
1237 in competition among plants. *Oecologia* 113:447–455.

1238 Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D.
1239 Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M.
1240 Fabrika, T. A. Nagel, and C. P. O. Reyer. 2017. Forest disturbances under climate
1241 change. *Nature Climate Change* 7:395–402.

1242 Shugart, H. H. 1984. A theory of forest dynamics: The ecological implications of forest
1243 succession models. Springer-Verlag, New York.

1244 Simioni, G., G. Marie, and R. Huc. 2016. Influence of vegetation spatial structure on growth
1245 and water fluxes of a mixed forest: Results from the NOTG 3D model. *Ecological*
1246 *Modelling* 328:119–135.

1247 Skovsgaard, J. P., and J. K. Vanclay. 2008. Forest site productivity: a review of the evolution
1248 of dendrometric concepts for even-aged stands. *Forestry* 81:13–31.

1249 Strigul, N., D. Pristinski, D. Purves, J. Dushoff, and S. Pacala. 2008. Scaling from trees to
1250 forests: tractable macroscopic equations for forest dynamics. *Ecological Monographs*
1251 78:523–545.

1252 TEEB. 2010. The Economics of Ecosystems and Biodiversity Ecological and Economic
1253 Foundations. Page (P. Kumar, Ed.). Earthscan, London and Washington.

1254 Toïgo, M., T. Perot, B. Courbaud, B. Castagneyrol, J.-C. Gégout, F. Longuetaud, H. Jactel,
1255 and P. Vallet. 2018. Difference in shade tolerance drives the mixture effect on oak
1256 productivity. *Journal of Ecology* 106:1073–1082.

1257 Trouvé, R., J.-D. Bontemps, I. Seynave, C. Collet, and F. Lebourgeois. 2015. Stand density,
1258 tree social status and water stress influence allocation in height and diameter growth of

- 1259 *Quercus petraea* (Liebl.). *Tree Physiology* 35:1035–1046.
- 1260 Ulrich, E. 1997. Organization of forest system monitoring in France-the RENECOFOR
1261 network. Page World Forestry Congress. Antalya, Turkey.
- 1262 Vanoni, M., M. Cailleret, L. Hülsmann, H. Bugmann, and C. Bigler. 2019. How do tree
1263 mortality models from combined tree-ring and inventory data affect projections of forest
1264 succession? *Forest Ecology and Management* 433:606–617.
- 1265 Verdone, M., and A. Seidl. 2017. Time, space, place, and the Bonn Challenge global forest
1266 restoration target. *Restoration Ecology* 25:903–911.
- 1267 Verheyen, K., M. Vanhellemont, H. Auge, L. Baeten, C. Baraloto, N. Barsoum, S. Bilodeau-
1268 Gauthier, H. Bruelheide, B. Castagneyrol, D. Godbold, J. Haase, A. Hector, H. Jactel, J.
1269 Koricheva, M. Loreau, S. Mereu, C. Messier, B. Muys, P. Nolet, A. Paquette, J. Parker,
1270 M. Perring, Q. Ponette, C. Potvin, P. Reich, A. Smith, M. Weih, and M. Scherer-
1271 Lorenzen. 2016. Contributions of a global network of tree diversity experiments to
1272 sustainable forest plantations. *Ambio* 45:29–41.
- 1273 Verkerk, P. J., J. B. Fitzgerald, P. Datta, M. Dees, G. M. Hengeveld, M. Lindner, and S.
1274 Zudin. 2019. Spatial distribution of the potential forest biomass availability in Europe.
1275 *Forest Ecosystems* 6:5.
- 1276 Vidal, J.-P., E. Martin, L. Franchistéguy, M. Baillon, and J.-M. Soubeyroux. 2010. A 50-year
1277 high-resolution atmospheric reanalysis over France with the Safran system. *International*
1278 *Journal of Climatology* 30:1627–1644.
- 1279 Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007.
1280 Let the concept of trait be functional! *Oikos* 116:882–892.
- 1281 Wehrli, A., P. J. Weisberg, W. Schönenberger, P. Brang, and H. Bugmann. 2007. Improving
1282 the establishment submodel of a forest patch model to assess the long-term protective
1283 effect of mountain forests. *European Journal of Forest Research* 126:131–145.

1284 Williams, L. J., A. Paquette, J. Cavender-Bares, C. Messier, and P. B. Reich. 2017. Spatial
1285 complementarity in tree crowns explains overyielding in species mixtures. *Nature*
1286 *Ecology & Evolution* 1:0063.
1287

1288 **Tables legend**

1289

1290 Table 1: Description of the species parameters in ForCEEPS. References refer to the literature
1291 used to calibrate all or part of the species for the specific parameter.

1292

1293 Table 2: ForCEEPS accuracy in predicting tree growth across all species and for each species
1294 separately, through Pearson correlation, root mean square error (RMSE) and average bias (AB)
1295 between observed and predicted tree growth. Significance of the Pearson correlation coefficient
1296 (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; *ns*: $p > 0.05$).

1297

1298 Table 3: ForCEEPS accuracy in predicting stand productivity and test of the differences
1299 between the various versions tested:

1300 (a) Across all plots, though through Pearson correlation, root mean square error (RMSE)
1301 and average bias (AB) between observed and predicted stand productivity. *Full*:
1302 ForCEEPS simulations with the new crown length module, climatic constraints on tree
1303 growth and interspecific variability in parameter *ShTols*; *noCrownL*: ForCEEPS
1304 simulations without the new crown length module; *noClim*: ForCEEPS simulations
1305 without climatic constraints on tree growth; *noVarShTol*: ForCEEPS simulations
1306 without interspecific variability in parameter *ShTols*. %RMSE: percentage difference
1307 between the RMSE of the version tested and the “full” version.

1308 (b) For each species taken separately for the full version, through Pearson correlation, root
1309 mean square error (RMSE) and average bias (AB) between observed and predicted
1310 stand productivity tree growth.

1311 Significance of the Pearson correlation coefficient (***: $p < 0.001$; **: $p < 0.01$; *: $p <$
1312 0.05 ; *ns*: $p > 0.05$).

1313 Table 1

Parameter	Details	Unit	Example (<i>Fagus sylvatica</i>)	Calibration	References
f_s	Foliage type	Unitless E - evergreen - or D - deciduous and a number between 1 and 5	D3	Literature	Rameau et al. 1989; Didion et al. 2009
$Hmax_s$	Maximum height	m	50	Literature + NFI	Rameau et al. 1989, 2008
s_s	Allometry	Unitless	76	Literature + NFI	Didion et al. 2009
g_s	Optimal growth rate	Unitless	260	Literature + NFI	Didion et al. 2009
$Amax_s$	Maximum age	years	400	Literature	Rameau et al. 1989; Bugmann 1994
$Ddmins$	Minimal required annual or seasonal degree-days sum	°C	841	Literature	San-Miguel-Ayanz et al. 2016
$DrTols$	Drought tolerance index, to be compared to the evapotranspiration deficit based on a bucket model of soil moisture	Continuous index with values between 0 (sensitive) to 1 (tolerant)	0.25	Literature	Ellenberg and Mueller-Dombois 1966; Ninemets and Valladares 2006; Rameau et al. 1989, 2008
$Nreq_s$	Soil nitrogen requirement	Integer Index with values between 1 (weak requirements) to 5 (strong req.)	2	Literature	Ellenberg and Mueller-Dombois 1966; Bugmann 1994
$ShTols$	Shade tolerance	Integer index with values between 1 (shade tolerant) to 9 (shade intolerant)	1	Literature	Ellenberg and Mueller-Dombois 1966; Ninemets and Valladares 2006; Rameau et al. 1989, 2008
$ShTol_seedling_s$	Shade tolerance of seedlings, to be compared to the relative amount of light reaching the ground	Continuous index with values between 0 (tolerant) to 1 (sensitive)	0.05	Literature	Ellenberg and Mueller-Dombois 1966; Ninemets and Valladares 2006; Rameau et al. 1989, 2008
$Wtmin_s$	Monthly minimum winter temperature tolerated for regeneration (°C)	°C	-6	Literature	Didion et al. 2009 ; San-Miguel-Ayanz et al. 2016
$Wtmax_s$	Monthly maximum winter temperature tolerated for regeneration	°C	9	Literature	Didion et al. 2009 ; San-Miguel-Ayanz et al. 2016
Br_s	Browsing susceptibility of seedlings	Integer index with values between 1 (less susceptible) to 5 (more susceptible)	3	Literature	Didion et al. 2009

1314

1315 Table 2

	All trees	<i>F. sylvatica</i>	<i>Q. petraea</i>	<i>Q. robur</i>	<i>A. alba</i>	<i>P. abies</i>	<i>P. sylvestris</i>	<i>P. pinaster</i>	<i>Q. ilex</i>	<i>P. halepensis</i>
Ntrees	2662	877	272	183	367	319	323	197	91	34
Nplots	82	16	16	10	9	9	11	6	3	2
Pearson r	0.72***	0.77***	0.66***	0.65***	0.74***	0.603***	0.491***	0.561***	0.616***	0.694***
RMSE	0.0012	0.0009	0.0011	0.0014	0.0014	0.0027	0.001	0.0014	0.001	0.0005
AB	0.124	-0.024	-0.050	0.334	-0.227	0.252	0.367	0.898	-0.073	0.481

1316

1317

1318 Table 3
 1319
 1320 (a)

	Full	noCrownL	noClim	noVarShTol
Nplots	82	82	82	82
Pearson	0.79***	0.69***	0.76***	0.80***
RMSE	0.019	0.022	0.032	0.035
%RMSE		15.43	69.68	85.11
AB	0.045	-0.102	0.599	0.363

1321
 1322
 1323
 1324 (b)

	<i>F. sylvatica</i>	<i>Q. petraea</i>	<i>Q. robur</i>	<i>A. alba</i>	<i>P. abies</i>	<i>P. sylvestris</i>	<i>P. pinaster</i>	<i>Q. ilex</i>
Nplots	16	16	10	9	9	11	6	3
Pearson	0.64*	0.69**	0.71**	0.86**	0.54.	0.83**	0.72.	0.76 ns
RMSE	0.013	0.016	0.013	0.020	0.003	0.015	0.034	0.001
AB	0.031	-0.167	0.241	-0.015	0.202	-0.070	0.503	-0.187

1325
 1326

1327 **Figures legend**

1328

1329 Figure 1. Summary of the workflow of the study. This figure illustrates the sequence of the
1330 main steps of the study.

1331

1332 Figure 2. Predicted (by ForCEEPS) against observed mean annual tree basal area increment
1333 (BAI) for all considered trees (over 82 sites) and the 5 repetitions. The plain black line is the
1334 regression line of the linear model of the relationship between observed and predicted tree
1335 growth, with confidence interval represented with the grey dashed lines; the dashed red line is
1336 the 1:1 line. Statistics associated: see Table 2.

1337

1338 Figure 3. Predicted (by ForCEEPS) against observed mean annual stand basal area increment
1339 (BAI) for the 82 sites, using different model configurations:

1340 A- ForCEEPS simulations with the new crown length module, climatic constraints on tree
1341 growth and interspecific variability in shade tolerance (parameter *ShTol_s*).

1342 B- ForCEEPS simulations without the new crown length module.

1343 C- ForCEEPS simulations without climatic constraints on tree growth.

1344 D- ForCEEPS simulations without interspecific variability in parameter *ShTol_s*.

1345 For all panels: the plain black line is the regression line of the linear model of the relationship
1346 between observed and predicted stand productivity, with confidence interval represented with
1347 the grey dashed lines; the dashed red line is the 1:1 line. Statistics associated: see Table 3-a.

1348 Colour code for the species as follows:

1349

- *Fagus sylvatica*
- *Quercus robur*
- *Quercus petraea*
- *Quercus ilex*
- *Abies alba*
- *Picea abies*
- *Pinus sylvestris*
- *Pinus pinaster*
- *Pinus halepensis*

1350

1351

1352 Figure 4. (A) Simulated basal area (m² per ha) at the end of long-term ForCEEPS simulations
 1353 along sites representing a gradient of environmental conditions from cold and moist alpine
 1354 conditions (left) to warm-dry Mediterranean conditions (right). The site names and conditions
 1355 are stated in Table S3, with Aa (*A. alba*); Pa (*P. abies*); Ps (*P. sylvestris*); Cb (*C. betulus*); Fs
 1356 (*F. sylvatica*); Qp (*Q. petraea*); Qb (*Q. pubescens*); Qr (*Q. robur*); Pp (*P. pinaster*); Ph (*P.*
 1357 *halepensis*); Qi (*Q. ilex*); MounGymno (mountainous gymnosperm species including *L.*
 1358 *decidua* and *P. cembra*); MounBroad (mountainous broadleaf species including *S. aria*, *S.*
 1359 *aucuparia* and *U. glabra*); OtherBroad (broadleaf species including *B. pendula*, *F. excelsior*
 1360 and *P. tremula*). (B) Distribution of the 15 tested sites in the PNV diagram of the supposed
 1361 dominating species (built according to mean annual temperature and annual precipitation sum).
 1362 Green dots: sites for which the dominating species in the simulated communities were
 1363 accurately predicted according to the PNV diagram; Blue dots: sites for which at least one of
 1364 the dominating species was accurately predicted but with another dominating species not
 1365 supposed to dominate according to PNV diagram. Red dots: sites in which the simulated
 1366 community was dominated by other species than supposed by the PNV diagram. Numbers refer
 1367 to the site number (see Table S3). PNV dominating species are Pc (*P. cembra*), Pu (*P. uncinata*);

1368 Aa (*A. alba*); Pa (*P. abies*); Fs (*F. sylvatica*); Qp (*Q. petraea*); Qr (*Q. robur*); Pp (*P. pinaster*);
1369 Ph (*P. halepensis*); Qi (*Q. ilex*).

1370

1371 Figure 5. Correlations between key ForCEEPS parameters and ecophysiological traits extracted
1372 from the literature (see Appendix E). Blue dots: Angiosperms; orange dots: Gymnosperms.

1373 Associated statistics are presented in Table S5.

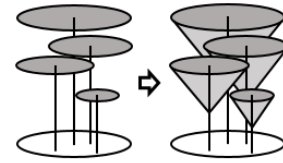
1374

1375

1376 Figure 1
 1377
 1378

STEP 1

Development of a new module for competition for light



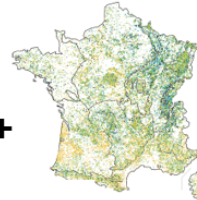
STEP 2

Calibration of species parameters
 For the main tree species in France



Literature

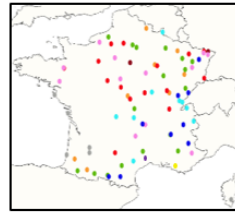
+



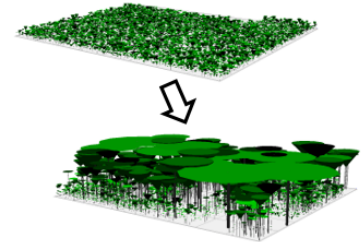
NFI data

STEP 3

Simulations for validation



Simulating tree and stand productivity
 on experimental sites
 (RENECOFOR + Puéchabon + Font Blanche)



Simulating long-term community
 composition along a gradient of sites



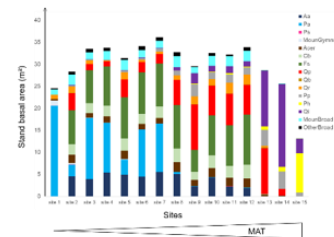
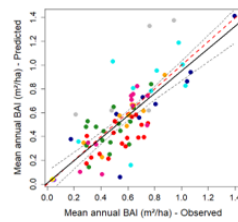
Validation of ecosystem functioning
 (monospecific stands)



Validation of species composition
 (mixed stands)

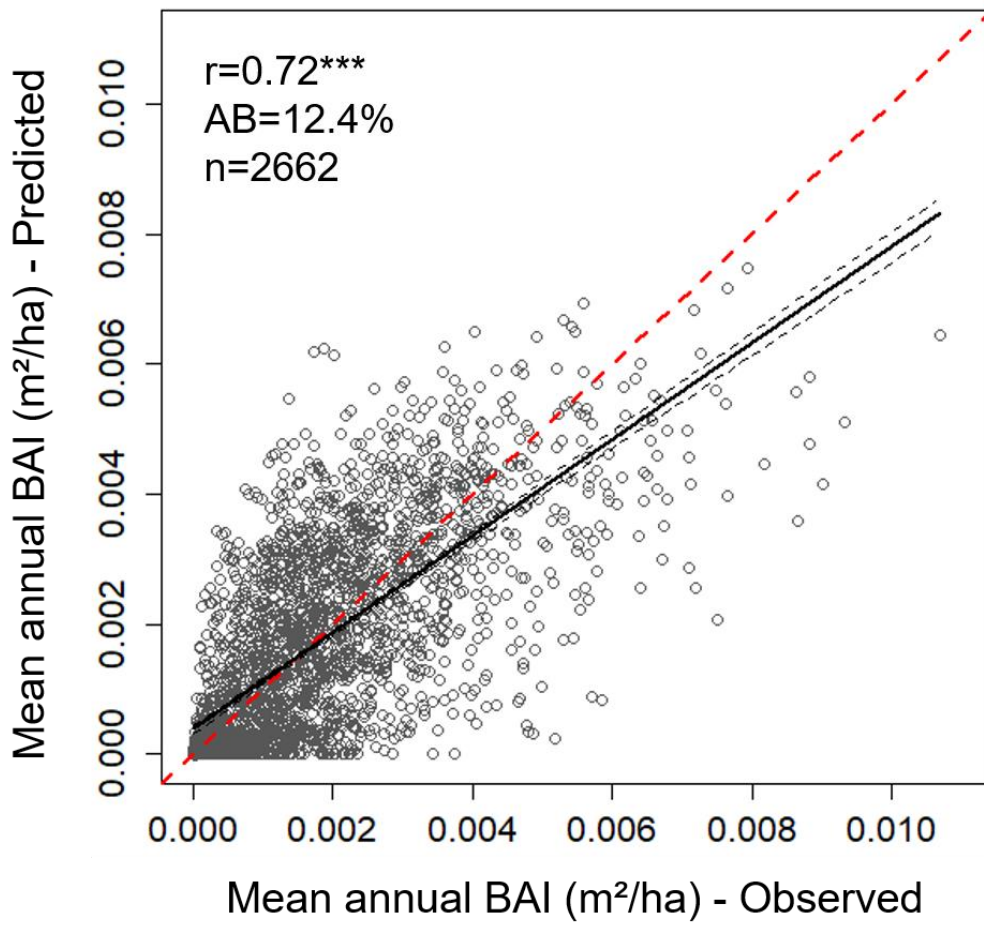
STEP 4

Validation of ForCEEPS

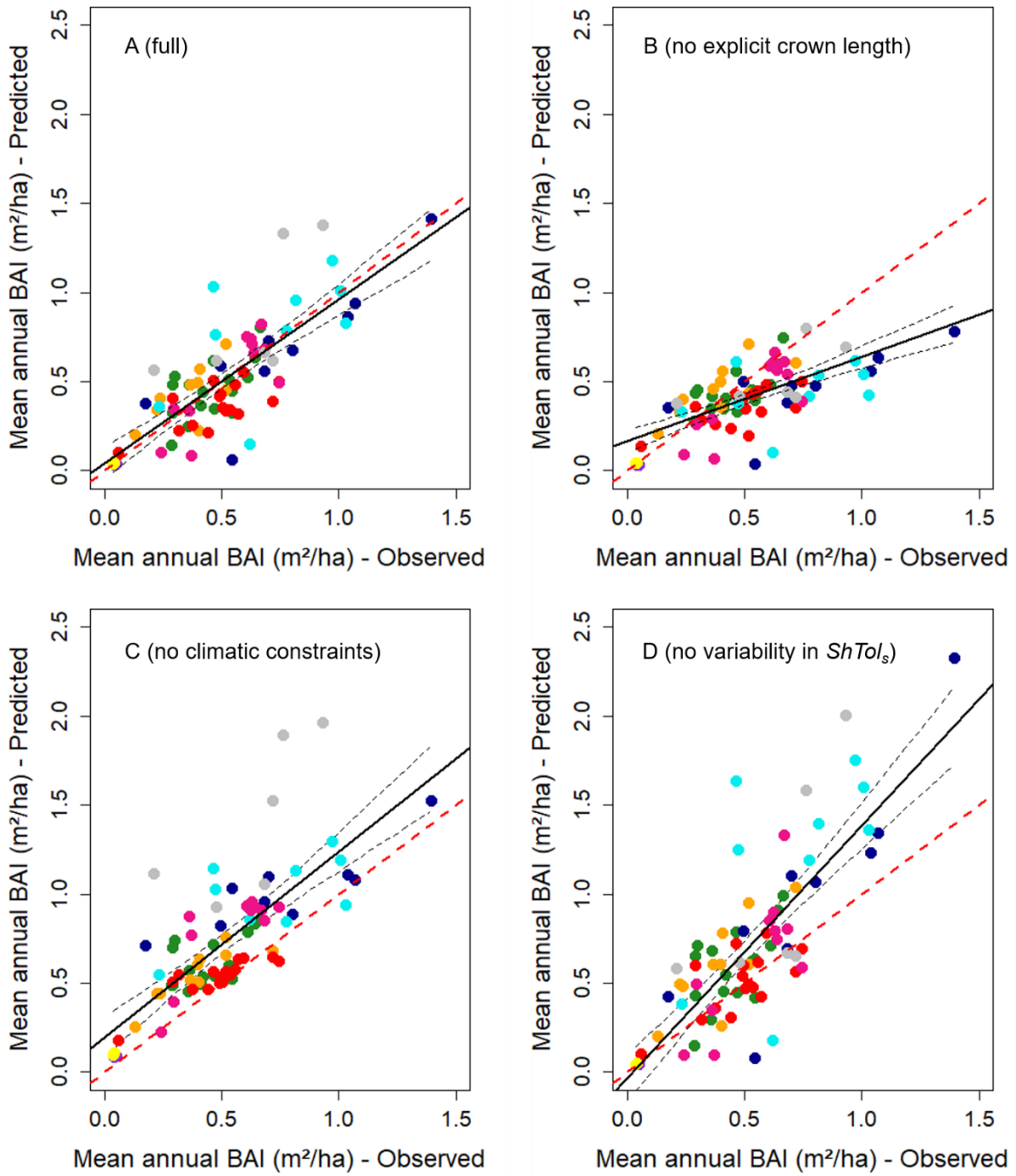


- + Testing the new module for competition for light
- + Testing the effect of environmental conditions
- + Testing the role of the shade tolerance parameter

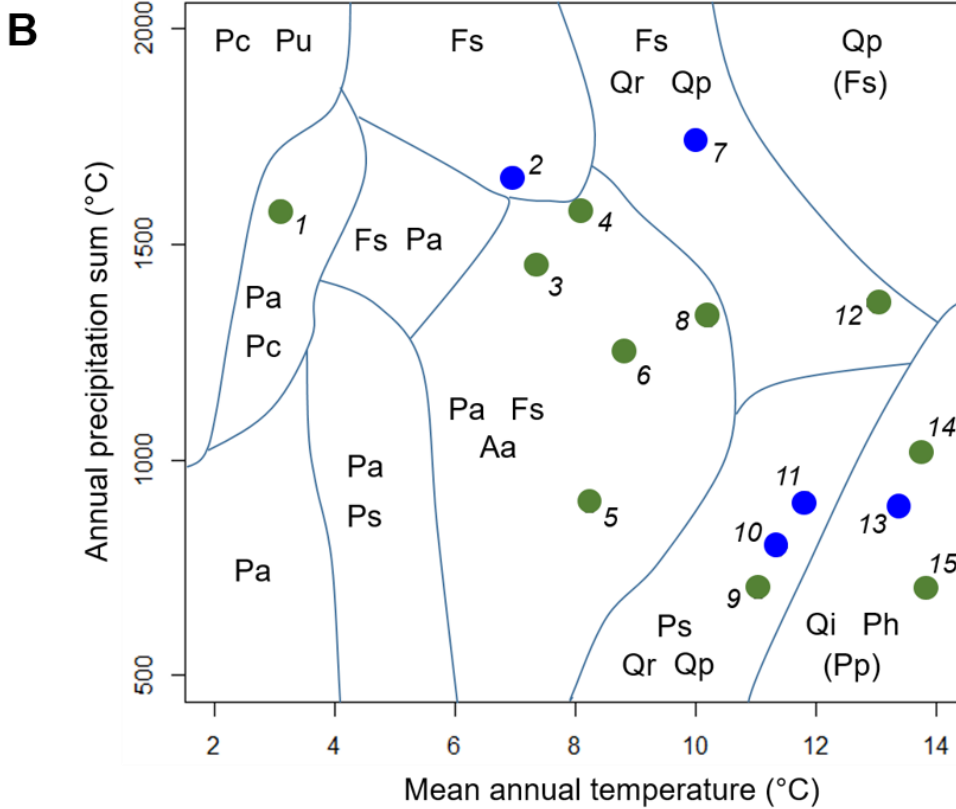
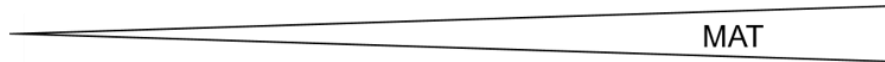
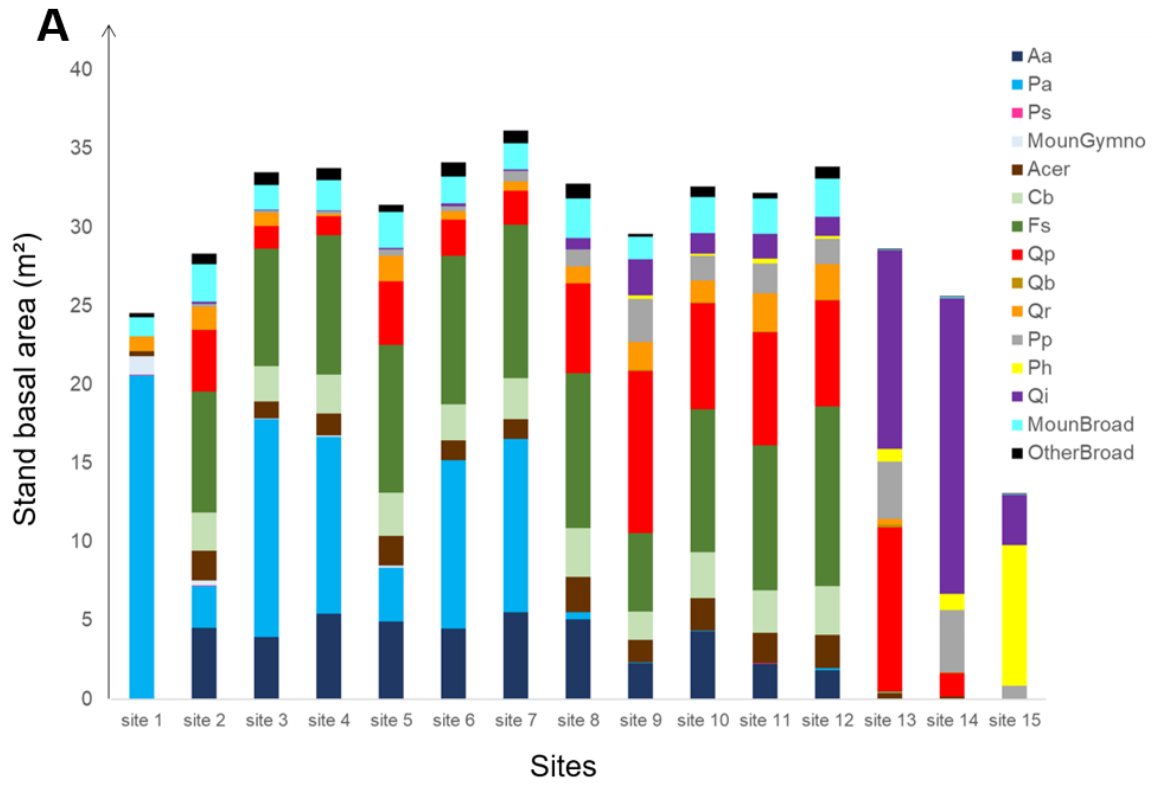
1379
 1380



1382
1383

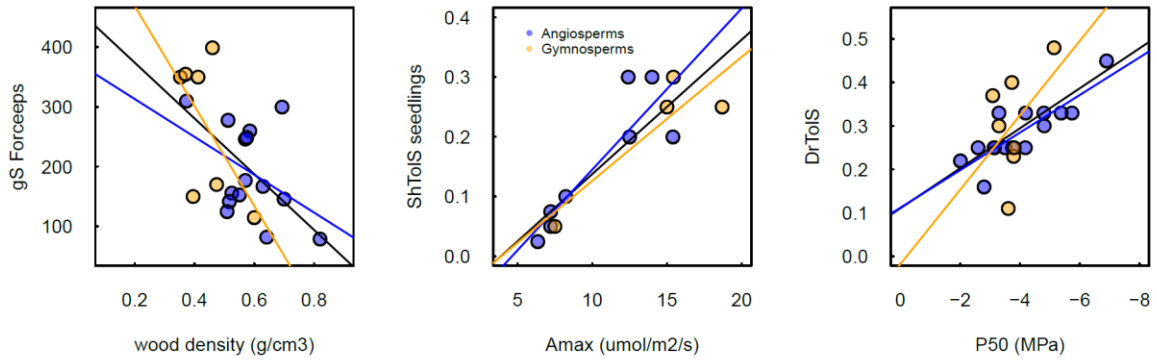


1385
1386
1387
1388



1391 Figure 5

1392



1393

1394

1395

1396	Appendices of Morin et al.
1397	
1398	Appendix A. Description of the model ForCEEPS.
1399	
1400	
1401	Appendix B. Supplementary Tables.
1402	S1. Parameter values for all species
1403	S2. Number of plots and trees per species considered in the analyses
1404	S3. Sites used in the PNV analysis
1405	S4. All repetitions – tree level
1406	S5. Correlations between ForCEEPS parameters and ecological traits at the
1407	interspecific level
1408	
1409	Appendix C. Supplementary Figures.
1410	S1. Representation of tree crowns in ForCEEPS
1411	S2. Distribution of the sites according to climate variables or indices
1412	S3. Repetitions at the tree level
1413	S4. Results at the tree level per species
1414	S5. Results at the stand level per species
1415	S6. Residuals of simulated tree growth against tree diameter
1416	S7. Residuals of simulated stand growth against stand basal area
1417	
1418	Appendix D. Additional information about field data for calibration.
1419	
1420	Appendix E. Information about ecophysiological traits
1421	