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► To cite this version:

Jens Joschinski, Isabelle Boulangeat, Mariasole Calbi, Thomas E Hauck, Verena Vogler, et al.. The ECOLOPES PLANT MODEL : a high-resolution model to simulate plant community dynamics in cities and other human-dominated and managed environments. 2024. hal-04711560

HAL Id: hal-04711560

<https://hal.science/hal-04711560v1>

Preprint submitted on 27 Sep 2024

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2 The ECOLOPES PLANT MODEL : a high-resolution model to
3 simulate plant community dynamics in cities and other human-
4 dominated and managed environments

5

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15 Abstract

16 Cities and urbanized areas have become an important habitat for organisms. Although nature
17 can provide multiple ecosystem services to humans, urban planning and architecture often do
18 not adequately consider the ecological needs of species. In ECOLOPES we envision buildings,
19 and in particular building envelopes, to be a joint habitat for humans, plants, animals and
20 microbiota as equally relevant stakeholders. A centerpiece of the planning and design tools
21 that ECOLOPES provides is a joint soil-plant-animal community model. We present the first
22 prototype of the ECOLOPES PLANT (community) MODEL that responds to 3-dimensional
23 (building) geometry and management, show potential applications as a stand-alone model,
24 and discuss its technical and conceptual limitations that are yet to be overcome.

25

26 **Keywords:** architectural design, biodiversity, ecological modelling, urban ecosystems

27

28 Introduction

29 Biodiversity provides multiple tangible and intangible benefits to society, including e.g.
30 psychological (Fuller et al., 2007) and medical (Erwin et al., 2010) remedies, agricultural
31 benefits (Dainese et al., 2019) and sources of economic wealth (Echeverri et al., 2022). The
32 largest ecological benefit of biodiversity is probably the sustenance of ecosystem functioning,
33 and of its temporal stability (e.g., Cardinale et al., 2012; Tilman & Downing, 1994). Overall, a
34 sustained biodiversity loss (mass extinction) would have far-reaching consequences, including
35 on the ecology and long-term evolution of surviving taxa (Jablonski, 2001).

36 Biodiversity is indeed rapidly declining globally (Díaz et al., 2019; Hallmann et al., 2017; Pereira
37 et al., 2010; van Klink et al., 2024), at a rate comparable to historic mass extinctions (Ceballos
38 et al., 2015) and thus of major concern for society (United Nations, 2015, SDG 14 & 15).

39 Patterns and drivers of biodiversity loss differ among taxa (Sánchez-Bayo & Wyckhuys, 2019),
40 but land use and land cover change is globally the largest cause of biodiversity decline (IPBES,
41 2019; Jaureguiberry et al., 2022). Humans are responsible for the changes in land use and land
42 cover with highest impact on biodiversity, most notably agricultural intensification (Egli et al.,
43 2018; Kehoe et al., 2017) and urbanization (McDonald et al., 2020; Seto et al., 2012). Stopping
44 or even reverting the trends in land use and land cover change is a major societal challenge
45 on its own (United Nations, 2015, SDG 2 & 11), and solutions that revert the trend would
46 benefit not only biodiversity but also food security and human health and well-being.

47 The impacts of land use and land cover changes can be moderated by thoughtful interventions
48 (e.g., hedges for connectivity, crop diversity, wildflower strips) that can significantly increase
49 ecological stability and functioning without large negative economic impacts (Bommarco et
50 al., 2013). Similarly, simple and cost-efficient measures (e.g. reduced management) can

51 improve biodiversity and ecological functioning in heavily urbanized areas (Threlfall et al.,
52 2017; Vega & Küffer, 2021). Yet, better results may be achieved when ecology is integrated
53 and made an explicit objective, both in agriculture (organic farming) and in architecture and
54 urban planning (e.g., regenerative design, net-positive design, biophilic design), as early
55 consideration allows mediating conflicting objectives (Birkeland, 2020) and considering the
56 multiscale nature of ecological processes (Beninde et al., 2015).

57 The ECOLOPES (ECOlogical building enveLOPES) project aims to integrate ecology as early as
58 possible into the design process, with the aim to design ecologically sound buildings (Weisser
59 et al., 2023). In contrast to existing approaches, ECOLOPES considers not only the ecosystem
60 services that urban green provides to humans, but also the perils and chances that
61 architecture delivers to plants, animals and the microbiota. As such, it represents a radical
62 change of view, from an anthropocentric view towards a vision in which non-human
63 stakeholders are equally considered. Consequently, the ideal *ecolope* does not resemble a
64 garden or park, but is a self-managed and functional ecosystem that requires no or only very
65 little management. Moreover, ECOLOPES does not only conceptually consider ecological
66 needs, but also provides the tools for a technical, integrated analysis that can be put in
67 practice by landscape planners and architects (<https://gitlab.com/ecolopes-team>). One of the
68 key outcomes of ECOLOPES will be a coupled ecological model, which jointly simulates plant,
69 animal and (soil) microbe communities, their interaction, and how the community (and its
70 temporal change) is affected by architectural features and urban planning decisions. This
71 ecological model can in turn be combined with other computational tools to become the
72 centerpiece of a data-driven design recommendation system, and help lowering the conflict
73 between needs of humans and of other stakeholders.

74

75 We here present the first prototype of the ECOLOPES PLANT MODEL, as one of the parts of the
76 envisioned joint ecological model. This C++ - Model is derived from the model Fate-HD
77 (Boulangeat et al., 2014) and simulates plant communities in a 3-dimensional environment.
78 We strictly limit ourselves to a technical description and discussion of capabilities of the model
79 itself, as the integration into a complex computational workflow (plugin for Rhino®, McNeel
80 Europe) is not finished yet. A discussion of the model (or any successors) in an applied context
81 will accordingly be published separately.

82

83 [Methods](#)

84 The ECOLOPES PLANT MODEL is a stand-alone tool that models plant dynamics at high resolution
85 and which will also be integrated into the computational workflow of ECOLOPES. We here
86 summarize the model by describing its modeling objectives, concepts and required inputs. We
87 also demonstrate the model's general utility with the help of (manually created) 2D and 3D
88 inputs and a visualization in R. The full description of the model can be found in the appendix.
89 This description follows the ODD (Overview, Design concepts, Details) protocol for describing
90 individual- and agent-based models (Grimm et al., 2006, as updated by Grimm et al., 2020).

91

92 [Objectives and novelty](#)

93 The ECOLOPES PLANT MODEL aims to predict the presence, abundance and community
94 dynamics of different types of plants, usually clustered into Plant Functional Groups (PFGs). It
95 is derived from the Fate-HD community model (Boulangeat et al., 2014). In short, Fate-HD is
96 a landscape model that combines species distribution modeling with coarse-grained
97 (generalized) process-based modeling, thus achieving a balance between general applicability

98 and accuracy. The outputs of Fate-HD are not to be taken at face value, but indicate relative
99 shifts in community composition over time.

100 The ECOLOPES PLANT MODEL inherits most of the concepts of Fate-HD, but repurposes it to
101 evaluate the effect of microenvironmental conditions on community composition and
102 succession, in a 3-dimensional environment. Like its predecessor, the current version captures
103 relative community shifts, but in contrast to Fate-HD the long-term aim is a more accurate
104 prediction of plant biomass in absolute terms. Moreover, the ECOLOPES PLANT MODEL is meant
105 to be combined with other tools, e.g., an animal model that predicts animal community
106 dynamics based on the plant community, and hence requires a high degree of interoperability
107 and flexibility. This version of the model serves as backbone for future refined versions and
108 identifies technical constraints for providing more accurate results. To this aim, we revised the
109 technical implementation while conserving almost all concepts from the precursor, except for
110 light competition, which is further elaborated in the discussion.

111 In summary, this version of the model is not meant to provide information about biomass
112 distribution in absolute numbers yet, but it allows showcasing the technical feasibility and
113 utility of a 3D community model, and it allows identifying conceptual challenges that need to
114 be solved in the future.

115

116 [Entities and scale](#)

117 The model is designed for use in urban environments, and it simulates community dynamics
118 over the typical lifespan of a building envelope; its spatial resolution is fixed at 1m x 1m x 1m,
119 while the extent is variable but shall be in the order of 100 x 100 x 10 m (length, width,
120 elevation). It is made up of cubic cells in which a plant community can thrive. The cubic cell
121 itself is stratified, mimicking the stratification of plant communities. We chose four strata in

122 our tests, corresponding to herb, shrub, understory and canopy layers. Plants differ in
123 maximum sizes and growth forms (e.g. grasses vs. shrubs vs. trees), and hence both in the
124 number of strata they grow through and in the time they stay within each layer.

125 The principal agent of the model is the demographic composition of a local stand of plants of
126 the same species of functional group (i.e. not explicitly an individual plant). In lack of a better
127 wording, we will name this local aggregation of plants of the same taxonomic group but
128 different ages a deme (but without implying any genetic structure or local adaptation). The
129 deme itself consists of age cohorts of individuals, but individuals within an age cohort are not
130 uniquely identifiable (no inter-individual variation). Multiple demes of different functional
131 groups or taxonomic identity can potentially live together in a cell to create a community, and
132 each is defined by its own trait values (e.g., demographic traits' values, responses to
133 disturbances, etc; see Supp. S1, Table 4). The trait values have to be provided by the user, and
134 one way to overcome data limitations is the aggregation of functionally redundant species
135 into the same group, i.e., the creation of Plant Functional Groups (Boulangéat et al., 2012).

136 Plant composition dynamics is implemented through the temporal simulation of
137 demographical changes of the plant community (i.e., temporal changes of deme abundances)
138 in each stratum of the cells, also accounting for the simulated concomitant changes in light
139 availability (caused by changes in deme abundance). We use a slightly different and more
140 explicit concept of light in this model than the precursor Fate-HD, and we will elaborate the
141 differences in the discussion. Briefly put, light passes through the strata of the community and
142 gets reduced along the way. In contrast to Fate-HD, where it is not available light that is in the
143 reasoning but rather shading effect through the evolution of the canopy, in this model the
144 amount of available light is corrected by shading (e.g., by buildings). This ensures that shaded
145 cells fall earlier to "medium" or "low" light conditions and potentially exclude non-tolerant

146 PFGs. Furthermore, light may fall at an angle below 90°. If this is the case, it will partially pass
147 through the neighboring cell and is accordingly reduced by the neighbor’s plant abundance.
148 Apart from the dynamically changing light conditions, the plant demes also respond to the
149 following microenvironmental (cell) parameters that are usually provided as an input to the
150 model, adapted from the “habitat suitability” and “disturbance” modules of FATE-HD:

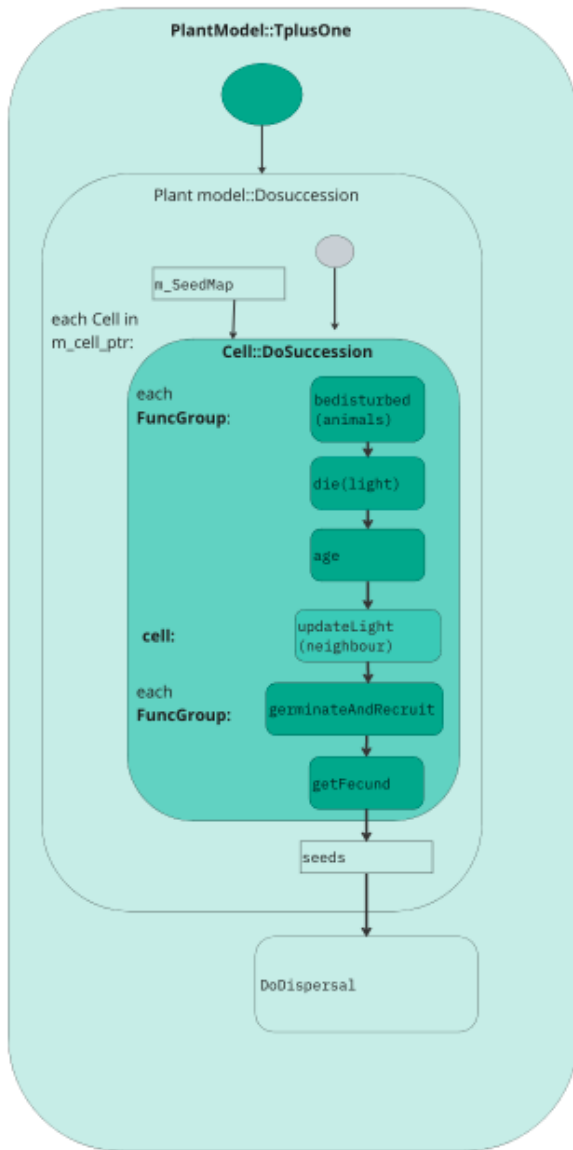
- 151 - *Soil depth*. The depth of the soil is a limiting factor for plants, especially deep-rooting
152 ones. Accordingly, plants whose rooting depth exceeds the soil depth are unable to
153 grow.
- 154 - *Soil class*. Plants differ in soil requirements and hence have different soil profiles. If the
155 soil class in a cell does not match the plant’s profile, the plant is unable to germinate
156 or grow.
- 157 - *Disturbance*. External, user-defined disturbances such as herbivory, fire or
158 management can impact population demography. The strength of the effect may differ
159 among PFGs.
- 160 - *Shading*. Shading caused by buildings or natural structures (cliffs) reduces available
161 light and thereby intensifies competition among PFGs (as explained above).

162
163 These four cell attributes are constant throughout the model run in the stand-alone version
164 of the new model. However, the model may also be compiled as a shared library (.dll), allowing
165 it to be embedded in other programs and models (not available under Windows). If used in
166 such a way, the inputs “soil class” and “disturbance” can be exchanged at every time step. This
167 allows, e.g., modeling directional and stochastic climate change through changes in the soil
168 class attribute.

169

170 Process overview

171



172

173 *Fig. 1: Process overview. The order of events is largely copied from Fate-HD, so that conceptual changes to the*
174 *model are kept to a minimum. Processes in this diagram match function names of code (see UML diagram in*
175 *Supp. S1); the deme is called FuncGroup in the code.*

176

177 The model largely works on individual cells (Fig. 1) and uses the process employed by Fate-

178 HD: in each time step, each plant deme is disturbed by a number of fixed, annual disturbances.

179 Depending on its PFG traits, each growth stage of a deme may react differently to the

180 disturbances, including not being affected at all. Then it is checked, separately for each

181 stratum, whether the current light conditions are sufficient. A common outcome is the death
182 of all lower plants, while the upper plants survive. Subsequently the deme ages by one time
183 step, potentially causing the oldest demographic group to die. Aging is followed by a
184 calculation of the new light conditions. Light is calculated based on the demography of the
185 whole community of the cell, and in contrast to FATE-HD, also of the neighboring cell if
186 enabled. This is actually more important for the targeted resolution (1m), as individuals could
187 spread over several cells. Germination and recruitment are then individually computed for
188 each deme, and the outcome is a number of newly produced seeds. These processes depend
189 on the current suitability of the cell, which is in turn determined by soil depth and soil class.
190 The newly dispersed seeds are not immediately placed back into the cell. Instead, all seeds
191 across the landscape are collected and then uniformly and randomly dispersed across the site.
192 The Fate-HD modules “soil”, “drought”, “fire” and “aliens” of Fate-HD were not ported to this
193 version, but can be emulated by other means; “disturbance” was reduced to removal of adult
194 plant material (no seed predation and no resprouting); and “dispersal” was simplified to
195 accommodate the smaller spatial scale. See appendix S1 for details.

196

197 [Input and output data, initialization](#)

198 The model requires the following information to run:

- 199 - Configuration parameters (12 variables, see Supp. S1 Table 3)
- 200 - Definition of Plant Functional Groups, including their response to disturbances (e.g.
201 management, animals) and soil (26 variables, see Supp. S1 Table 4)
- 202 - Microenvironmental information for each cell. This currently includes the amount of
203 shading, soil class and soil depth, and the amount of each (user-defined) disturbance.

204

205 The output of the model is an abundance value of each deme in each cell, for each time step
206 that was specified. The abundance values are unitless expressions to compare among PFGs,
207 but in the future are expected to correlate with plant biomasses (see discussion).

208 Special consideration needs to be given to sensible starting populations. Starting conditions
209 may include, e.g., a barren soil that gets colonized over time; a random starting population;
210 an initialization period of 1000 time steps on either of above, to achieve a stable community;
211 the use of ecological mapping to explicitly instantiate each plant with correct age; or a
212 combination of above. Longer initialization periods are in principle possible, but increase the
213 runtime of the model, while explicit instantiation requires further high-resolution data. We
214 thus decided to initialize the models with zero – and 1-year old plants from each PFG, with an
215 abundance of 1 to 100 (uniformly random) wherever the habitat is suitable. The model then
216 runs for five time steps to achieve more variation in the age distribution in each cell.

217 We are aware that the required inputs (shading, depth, soil classes, PFGs and configuration
218 parameters) are difficult to create manually, and that the manual use of the tool is tedious.
219 We provide a short user guide in the supplementary material (Supp. S2) to explain the
220 required inputs, and steps to perform and run the model, but we would like to emphasize that
221 separate tools and workflows are in preparation (led by Verena Vogler), which will
222 considerably simplify input creation and visualization of results in the future.

223

224 [Model testing](#)

225 We use the gtest framework (google.github.io/googletest/) for unit and integration tests, but
226 tests are currently limited to the most crucial functions (40 tests in 6 test suites), focusing in
227 particular on the completely revised higher-level classes. Although we also revised the model
228 architecture and class relationships, low-level functions were changed only very sparingly. We

229 assume that these low-level functions were already rigorously tested in the predecessor
230 model (Fate-HD) and performed only informal tests. Where applicable, we provide
231 suggestions for future revision (see “issues” in repository, tag “coding issues”).

232 The most informative test suite regards a model run on a landscape of 18 cells, covering
233 management, habitat suitability, and disturbance, but not soil depth; soil depth was, however,
234 tested informally and is known to produce valid results. We also disabled dispersal, because
235 it randomizes results and is inherently more difficult to test. Test results can be verified by
236 inspecting the file “PlantModelTestNoDisp.cpp” (folder “tests”) on the repository, or by
237 running the model with the file “test_noDisp.json” and comparing inputs and outputs
238 manually.

239

240 [Data preparation and visualization](#)

241 To demonstrate the model’s utility but also to emphasize its current limitations, we prepared
242 two examples. For both examples we created 10 Plant Functional Groups (PFGs) defining the
243 traits of the plants. We used 10 randomly drawn PFGs from a dataset that creates generic
244 PFGs with worldwide applicability (Calbi et al., 2024), but adapted and simplified them to our
245 use case. The PFGs differ in soil type and depth requirements and in parameters relating to
246 growth, but not in shade tolerance (table 1).

247 In the first example we use a 2-dimensional planar surface without shade. We defined two
248 management plans, called “mowing” and “tree pruning”, and applied them annually in the
249 western and in the eastern side of the site, respectively. Mowing affects the herbs, while
250 shrub/tree PFGs are affected by pruning. PFG “herbs_95” is not affected by either
251 management plan. In the other direction (north to south), we apply a gradient of soil depth
252 from 0 to 45 cm in steps of 5 cm.

253 The second example is a 3-dimensional input geometry: a cuboid with a size of 10 x 10 x 5 m
254 lies on a planar surface of 20 x 20 m. Light immediately north of the cuboid is reduced due to
255 shading (10 – 50% reduction). Two balconies are attached to the southern face of the cuboid,
256 creating also a low amount of shading underneath, and mimicking a more complex
257 topography. The soil has a depth of 50 cm on the ground and on the balconies, and a depth of
258 10 cm on the top of the cuboid; tiles along the walls of the cuboid do not contain any soil. We
259 further define two soil types, which we term “ground” and “roof”, and which are distributed
260 on the ground and on the cuboid, respectively. We provide an intermediate amount of general
261 management (0.5) everywhere.

262 The outputs are visualized using R version 4.4.0, “Puppy Cup”(R Core Team, 2024) and the
263 packages jsonlite (Ooms, 2014) , tidyverse (Wickham et al., 2019) and rgl (Murdoch et al.,
264 2024). The R script for the entire procedure is available in the repository and in Supp. S3.

265

266

267 *Table 1. Attributes of the 10 example PFGs. “Pruning” and “mowing” represent effect sizes of management*
 268 *decision (annual removal rates), for other parameters see supplementary material (Supp. S1). Light tolerance was*
 269 *the same for all PFGs (no tolerance for shade in any PFG, except in germinant stage).*
 270

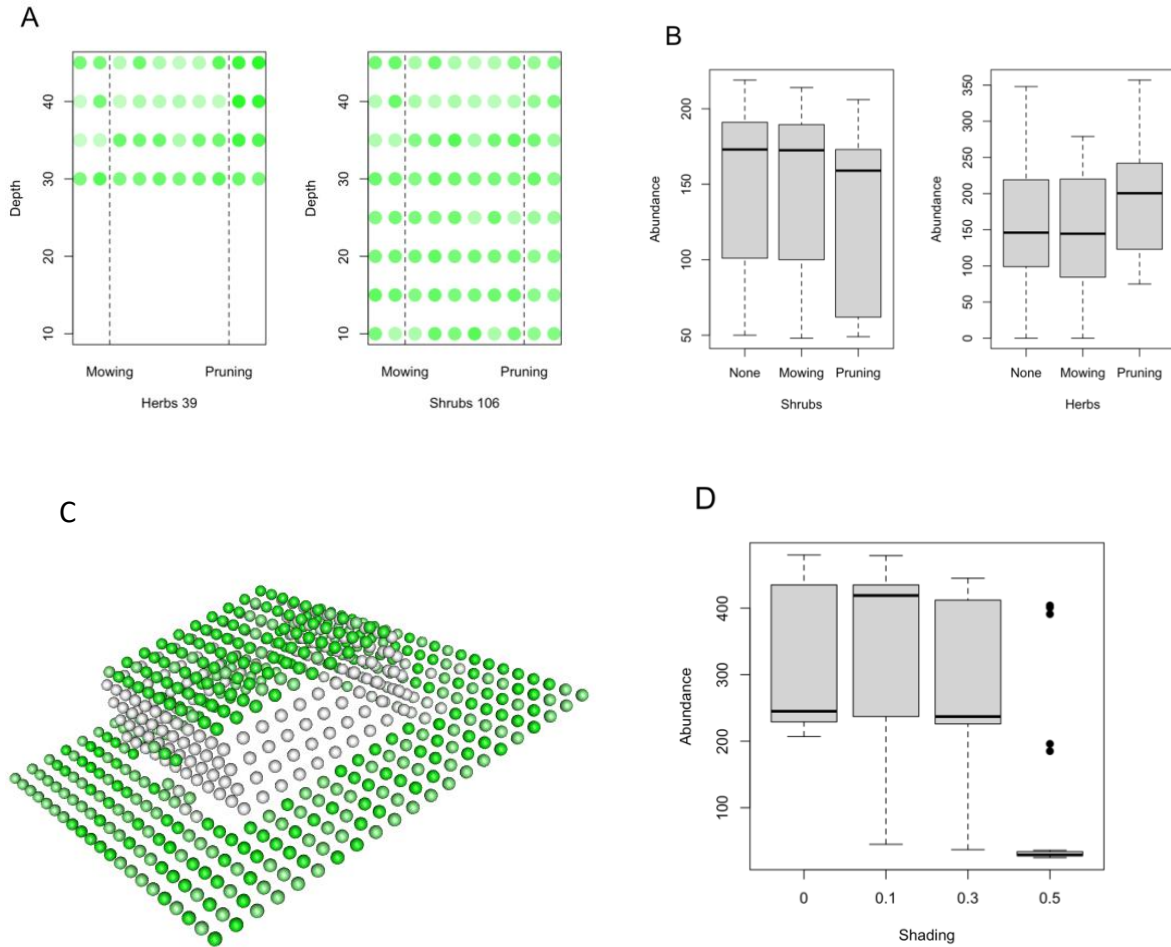
	herbs	herbs	herbs	herbs	herbs	shrubs	shrubs	shrubs	shrubs	shrubs
	153	39	72	93	95	_trees	_trees	_trees	_trees	_trees
matTime	3	3	3	3	3	5	3	3	3	3
LS	10	10	10	10	10	10	10	10	10	10
Abund	high	high	high	med	high	low	low	med	low	low
Immsize	0.8	0.8	0.8	0.5	0.8	0.5	0.5	0.5	0.5	0.01
MaxStratum	2	2	2	3	2	2	3	2	3	3
changeAge	0,1,2	0,1,2	0,1,2	0,1,1,5	0,1,2	0,1,1	0,1,1,5	0,1,5	0,1,1,5	0,1,1,1
PoolL	1	20	1	1	1	1	1	1	20	1
Fec	1	1	1	1	1	1	1	1	1	1
Shading	1	1	1	1	1	20	20	20	20	20
LAG	5,8,9	5,8,9	5,8,9	5,8,9	5,8,9	9,9,9	9,9,9	9,9,9	9,9,9	9,9,9
SoilTol	r,g	g	r	r	g	g,r	g	g,r	r	g
Depth	8	30	5	5	10	8	10	10	5	40
pruning	-	-	-	-	-	0.2	0.2	0.2	0.2	0.2
mowing	0.2	0.2	0.2	0.2	-	-	-	-	-	-

271 Results

272 All models since version 0.5.1 pass all unit and integration tests. This means that the model is
 273 fully functional and that the tested sections work within the specifications set out in the
 274 introduction and the ODD (see Supp. S1): the model creates a temporally changing and
 275 spatially variable plant community, which is affected by soil depth, soil class, shading
 276 conditions and disturbances (e.g. management decisions or herbivory); the effect of
 277 management on the communities can be calculated manually based on the inputs (as is done
 278 in the unit tests), while soil depth and soil class produce a binary response (match / mismatch).

279 The effect of shading on competition among PFG is non-linear and too complex to be included
280 in simple unit tests but can be verified by manual inspection of the results (see below).
281 In the first (2-dimensional) use case we observed a slight increase in total abundance
282 (summed over all PFGs) and soil depth (data not shown). The effect was, however, strongly
283 contingent on the PFGs that were used, and individual PFGs differed in patterns. For instance,
284 PFG herbs 39" only occurred on soils with a depth of 30 cm or more but did otherwise not
285 vary with soil depth (Fig. 2A, left). PFG "shrubs_trees 106" occurred from 10 cm onwards, but
286 its abundance decreased slightly with depth (Fig. 2A, right). Both groups of PFGs were also
287 affected by management, in particular by tree pruning, with differences in the direction of the
288 effect (Fig. 2B). There was no consistent change of abundances or community dynamics over
289 time, except that abundances were reduced over the first two time steps. There was strong
290 cyclic turnover in the community composition, however (data not shown). The period of the
291 cycles was two for all PFGs, so PFG abundances were at all times either in synchrony or exact
292 opposition. Cycles of adjacent cells were not coupled, unless light was allowed to pass at low
293 angles through neighboring cells – in this case, regular patterns occurred in the spatial
294 distribution of plants.

295 Using the second example topography presented in the methods, the spatial (3D)
296 configuration of the community mirrored the input topography, and the effects of light and
297 soil are readily visible in the outputs (Fig. 2C, D). For instance, shading (north of the cuboid)
298 caused lower total abundances (Fig. 2C) and herbal plants were disproportionately reduced
299 (herbs contributed on average 53.9% of the cell's PFGs abundance under full light, 12.2% in
300 shade; data not shown); further, all PFGs were missing along the walls of the cuboid, because
301 the soil class did not match with the PFG requirements. Overall, higher amounts of shading
302 had a strong effect on total PFGs abundance (Fig. 2D).



303

304

305 *Fig. 2: Graphical representation of modeling results. A) 2-dimensional planar surface without*
306 *shade and with soil depth gradient from north to south. Mowing occurs on the western side,*
307 *tree pruning on the eastern side. Color intensity indicates total abundance of the two PFGs*
308 *“herbs_39” and “shrubs_trees_106”, summed over time B) Comparison of summed PFGs*
309 *abundance between the three management types of A), separately for all shrubs and all herbs.*
310 *C) 3-Dimensional input geometry. Shading is present immediately north of the building, soil*
311 *depth and soil classes vary between roof and ground level, and general management is*
312 *present on the site (see methods for full description). For demonstration purposes, summed*
313 *abundance across all PFGs at time step 5 is shown. D) boxplot of summed abundance against*
314 *amount of shading for C).*

315

316 Discussion

317 Before discussing the constraints, limitations and broader relevance of the model, the first
318 question should be whether the model actually behaves as intended and conforms to the
319 specified goals and concepts.

320 The ECOLOPES PLANT MODEL is part of a complex computational toolchain, and while rigorous
321 software engineering principles are useful for nearly any individual-based model, their utility
322 exponentiates in a complex software setting with multiple components (e.g., Scheller et al.,
323 2010; Trisovic et al., 2022). Given these requirements, and its intended use in commercially
324 relevant applications, our model has to be held to particularly high standards regarding code
325 conformity and stability. It does by no means reach this much higher quality threshold yet,
326 and a provision of quality metrics (e.g. test coverage, cyclomatic complexity, static analysis
327 outputs) would be premature. Nevertheless, we embraced critical software engineering
328 principles wherever possible (encapsulation, clean code, assertions; full documentation and
329 logging; version control, automated integration and testing, portability; use of standard tools,
330 libraries and file formats) and we are confident that the software provides a reasonable basis
331 for future development. Indeed, the unit tests ensure alignment of the code with core model
332 specifications, and first simulation results look promising (Fig. 2). In the future more tests shall
333 be added, including not only those unit tests which are currently missing, but also full
334 integration tests that survey light competition outcomes in more detail. For now we suggest
335 that the model does largely behave as intended, though a risk for unforeseen bugs remains.

336 Unfortunately, biological research is somewhat detached from software engineering and
337 practitioners are frequently not trained in best practices (Vedder et al., 2021), nor is there
338 adequate consideration from funding and supervising bodies, or particular awareness in the

339 publication process (but see Freckleton, 2018). The resulting code quality and potential error
340 rate in biological research is disappointing (Darriba et al., 2018; Trisovic et al., 2022). On the
341 other hand, scientists are trained in critical analysis and should be able to detect major errors
342 and spurious results, somewhat mitigating the high risk for errors. We are confident that our
343 model can compete against this (low) baseline of model expectations, and we carefully
344 suggest that the model is ready for scientific use.

345 Having discussed the coherence of concepts and implementation, one may now ask whether
346 the conceptual decisions themselves are sensible. The concepts were in most parts borrowed
347 from Fate-HD and are defended in the model's description (Boulangeat et al., 2014), but there
348 are two important additional considerations which any reader and user of the model must be
349 made aware of.

350 First, the model's meaning of "light" differs slightly from that of Fate-HD. Fate-HD is a
351 landscape community model, which finds a balance between complexity and generality by
352 modeling general patterns at coarse resolution. Although both the model description
353 (Boulangeat et al., 2014) and the code of Fate-HD mention "light conditions" and "shading"
354 variables, they are meant to represent canopy effects, i.e., the integrated effect of shading,
355 humidity changes, and other abiotic and biotic factors. Similarly, the output of Fate-HD
356 (abundance) shall not be interpreted as biomass units in absolute numbers, but as a general
357 guidance regarding relative abundances of PFGs. A future version of the ECOLOPES PLANT MODEL
358 is, on the other hand, meant to provide accurate results in absolute values. The use of unitless
359 abundance and canopy values hinders transition to explicit biomasses, so light and shading
360 are taken more literally in the new model. This conceptual change has important
361 repercussions on the interpretation of results. For instance, in Fate-HD it was perfectly logical
362 if an understory plant required a canopy for survival (facilitation), because the canopy

363 provides a cooler and more humid climate; in the ECOLOPES PLANT MODEL it would not make
364 biological sense if a plant could survive under shaded, but not under full-light conditions. The
365 models hence differ in the expected parametrization.

366 Using the more literal interpretation of light/shading, the ECOLOPES PLANT MODEL was able to
367 make two further additions to the concepts and implementation. First, the amount of
368 available light is corrected by a shading index. This ensures that shaded cells fall earlier
369 to "medium" or "low" light conditions. Secondly, light may fall at an angle below 90°. If this is
370 the case, light will partially pass through the neighboring cell and is accordingly reduced by
371 the neighbor's plant abundance. These conceptual changes to light (along with their technical
372 implementation) ensure a more realistic treatment of shading, including shading by buildings
373 and other geometries (Fig. 2C). Nevertheless, while the new treatment of light is an important
374 step towards more explicit model outcomes in the future, we still advice against interpreting
375 them in absolute terms in the current version. For instance, within ECOLOPES (Weisser et al.,
376 2023) the model is expected to deliver «good enough» predictions on how building geometry
377 alters community structure, such that the model can be relied upon to provide suggestions
378 for improving building designs – but it cannot be used yet to calculate expected weight loads
379 on green roofs.

380 Secondly the ECOLOPES PLANT MODEL is applied on a much smaller spatial and temporal scale
381 than Fate-HD. In Fate-HD the community of each cell is usually a larger group of individuals,
382 but by reducing the spatial extent to a cube meter in this model, we simulate only a low
383 number of individual plants. This leads to a series of conceptual problems and mismatches
384 with reality:

385 1) in Fate-HD the highest stratum provides a canopy that (correctly) shades the lower strata,
386 potentially causing lower-growing plant material to die. Fate-HD does not strictly differentiate

387 between biomass and abundance of individuals (see Supp. S1, section 9), but because the
388 number of individuals per cell tends to be high, the lower-growing plant material of the same
389 PFG can statistically be interpreted as being a different individual (i.e., offspring). Our model
390 reduces the number of individuals per cell, and the abundance values must accordingly be
391 more strongly interpreted as biomass values of the same plant. This causes an unrealistic shift
392 from inter- to intra-individual competition;

393 2) Fate-HD does not model competition for space explicitly, so plants that grow within the
394 same stratum, which do not compete for light, do not compete with each other at all; in our
395 model the small spatial scale makes competition for space more important and should be
396 considered;

397 3) Plant material that grows to a higher stratum will hover in the air and its lower strata cast
398 no shade. This does not matter for the canopy calculation in Fate-HD (except at forest edges),
399 but becomes important when light enters at an angle;

400 4) Each plant community is confined to a single cell. Plant material that outgrows a cell does
401 not cast shade on the neighboring cell, so the results may become unreliable when the model
402 is used for larger PFGs;

403 5) The highest-growing plant material will usually determine the light conditions of the cell.
404 As long as the abundance in the highest stratum is high, nearly no plant material will grow
405 below. Because there is no inter-individual variation in lifespan, the abundance will change
406 suddenly, making room for other PFGs on the lowest stratum and causing the observed strong
407 population cycling on small time scales (see results), at least when the number of PFGs and
408 the variation in their demographics is low.

409 Overall, the reduction of the spatial scale warrants a revision of some of the key model
410 concepts. We argue that the core of the problem lies in the use of a (demographic) community

411 model for individual plants. Adding individuals with their own resource pools and (spatially
412 explicit) biomasses should solve various issues regarding light competition and may also
413 simplify parametrization. Moreover, a revision would solve various technical challenges
414 regarding data storage (see Supp. S1 and issues section in the repository). A later version of
415 an individual-based model could then add more realistic lighting calculations, including along
416 sloped surfaces and facades.

417 The question how well the conceptual decisions made here reflect reality must ultimately be
418 answered by parametrization and validation against real-world data. The parametrization is,
419 however, cumbersome in both Fate-HD and the new model. Six important parameters are set
420 via a configuration file (Light thresholds, abundances, fecundity; see Supp. S1, Table 3), and
421 14 further types of parameters (>25 entries) are specific for each PFG (Supp. S1, Table 4).
422 While some of the PFG parameters are straight-forward to understand (e.g. lifespan), others
423 do not have an intuitive or well-supported relationship with PFGs inherent features (size of
424 immatures relative to adults) or are not meant to represent a measurable entity (e.g., light
425 thresholds, a fecundity constant). Because the model parametrization by PFGs requires
426 considerable effort (Boulangéat et al., 2012), and because there are further technical and
427 conceptual issues to solve first (see above), we have so far opted against a separate
428 parametrization and validation of the model. We think that the validation performed by Fate-
429 HD shall still be mostly valid for larger spatial scales and lower resolutions, while for lower
430 scales and higher resolutions significant work is likely still required.

431 Having discussed the technical implementation and the concepts, the last remaining question
432 is the potential application of the model. As an integrated tool (Weisser et al., 2023), the
433 model is not, in fact, immediately useful in its own right, but requires other means to generate
434 inputs and visualize the results. Nevertheless, many researchers are proficient with R, and

435 when combined with R scripts, one can already create meaningful inputs and examine and
436 analyze the results. The simple example presented in the results shows that all key processes
437 are working (Fig. 2). First, PFGs differ in the spatial distribution along the site, according to soil
438 class and depth tolerances (Fig. 2A). Secondly, specific plot regions can be affected by
439 disturbances, and the effect of the disturbance is PFG-specific (Fig. 2B). Thirdly, the three-
440 dimensional setup of the site is adequately considered (Fig. 2C). For instance, total plant
441 biomass is reduced in shade (Fig 2D). The plant communities growing in the shade underneath
442 the balcony also differ from those growing above them, showing the potential to include
443 complex topographies. In summary, the example demonstrates that meaningful inputs can be
444 created manually, and visualized or analyzed with R.

445 The example presented here was on purpose very simple, as it requires the manual input of
446 data. Yet, the workflow could also be used for more complex use cases, for example to model
447 plant communities in alpine or otherwise topographically complex habitats. A digital elevation
448 model (DEM), analyzed with a shading function (e.g. hillShade, package raster) should provide
449 shading values, and combined with maps of soil depth and soil classes it should be able to
450 provide all necessary inputs for the model. Further, site-specific abiotic and biotic stressors
451 (e.g., strong winds, fire, herbivory pressure) could be added via custom-made disturbance
452 maps. The process is admittedly quite labor-intensive though and requires site-specific
453 scripting and tweaking of the data.

454 Conclusion

455 The current conceptual limitations notwithstanding, the model is technically ready and can
456 already provide a reasonable plant community that reacts to microenvironment and
457 topography. A tool built on this model or any successor that solves the presented issues

458 (Vogler, Grasshopper plugin in Rhino) can help visualizing the effect of the urban fabric on
459 plant communities, and especially with future improvements in mind, will help develop
460 buildings that promote ecological functions (Weisser et al., 2023).

461

462 [Author contributions](#)

463 AM and TH conceived the original idea and led the project. IB provided the original model

464 (FATE-HD) and contributed to the conceptual framework. VV provided help in data

465 structuring, inputs and outputs, and performed visual validations of earlier model outputs.

466 MC provided additional conceptual support, in particular regarding model parametrization.

467

468 [Acknowledgments](#)

469

470 We gratefully acknowledge funding by the EU H2020 FET-OPEN project ECOLOPES (Grant

471 agreement number 964414). We further thank Laura Windorfer, Victoria Culshaw, Wolfgang

472 Weisser and the whole ECOLOPES consortium for helpful discussions regarding the

473 conceptual development.

474

475

476 [Declaration of competing interests](#)

477

478 JJ and TH were employed by the company Studio Animal- Aided Design, VV by the company

479 McNeel & Associates. The remaining authors declare that the research was conducted in the

480 absence of any commercial or financial relationships that could be construed as a potential

481 conflict of interest.

482

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