Modelling understorey dynamics in temperate forests under global change— challenges and perspectives

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Abstract

The understorey harbours a substantial part of vascular plant diversity in temperate forests and plays an important functional role, affecting ecosystem processes such as nutrient cycling and overstorey regeneration. Global change, however, is putting these understorey communities on trajectories of change, potentially altering and reducing their functioning in the future. Developing mitigation strategies to safeguard the diversity and functioning of temperate forests in the future is challenging and requires improved predictive capacity. Process-based models that predict understorey community composition over time, based on first principles of ecology, have the potential to guide mitigation endeavours but such approaches are rare. Here, we review fourteen understorey modelling approaches that have been proposed during the last three decades. We evaluate their inclusion of mechanisms that are required to predict the impact of global change on understorey communities. We conclude that none of the currently existing models fully accounts for all processes that we deem important based on empirical and experimental evidence. Based on this review, we contend new models are needed to project the complex impacts of global change on forest understoreys. Plant functional traits should be central to such future model developments, as they drive community assembly processes and provide valuable information on the functioning of the understorey. Given the important role of the overstorey, a coupling of understorey models to overstorey models will be essential to predict the impact of global change on understorey composition and structure, and how it will affect the functioning of temperate forests in the future.

Key words

Herb layer, ground vegetation, mechanistic, process-based, forest ecosystems, review

1. Introduction

Multiple environmental pressures are threatening ecosystems, their functioning and the services they provide (MA, 2005). Although climate change and land cover change are the ones most visible at the global scale (e.g., via large scale deforestations, urbanization, shrinking glaciers and forest fires), also less-pronounced pressures, including subtle changes in temperature and precipitation regimes, deposition of anthropogenically fixed nitrogen and changes in ecosystem management are posing a serious threat. Substantial research effort has been invested into quantifying how these environmental pressures have changed over time and how they will change in the near future (e.g. Alkama and Cescatti, 2016; IPCC, 2014; Meiyappan et al., 2014; Seto et al., 2012). The next step, identifying how these pressures have affected ecosystems in terms of biodiversity (Didham et al., 2007), biotic interactions (Tylianakis et al., 2008) and ecosystem functioning (Balvanera et al., 2006), however, remains challenging (Franklin et al., 2016). The same holds for predicting future effects (e.g. Thom et al., 2017; Sala et al., 2000). Both tasks are complicated by potential interactions among global change drivers, potentially obscuring ecosystem responses to single pressures (Perring et al., 2016; Tylianakis et al., 2008).

Both statistical and process-based modelling can support these efforts by disentangling the effects of environmental pressures on ecosystems. Statistical models are predominantly suited to evaluate past impacts of global change, and can tell us how well-documented ecosystem changes correlate with environmental changes (Seidl et al., 2011a). Moreover, by analysing data gathered along different, preferably orthogonal, environmental gradients, the scope of statistical modelling can be further extended towards estimating how interactions among environmental change drivers have influenced ecosystem properties (Verheyen et al., 2017). However, since statistical models are always fit to a specific context, represented by the data used for modelling, they are less suited to predict future impacts or to explore the outcomes of alternative scenarios, especially if those scenarios involve new combinations of environmental conditions not observed in the past. For those tasks, process-based models are more suited (Seidl, 2017). By coupling processes at multiple temporal and spatial scales, scenario analyses, sensitivity analyses and experimentation *in silico* can provide an improved understanding of the underlying mechanisms and potential effects of global change (e.g. Cramer et al., 2001; Seidl et al., 2014).

Decades of progress in community ecology and mathematical modelling in combination with increasing data availability have led to the development of numerous process-based models for a wide variety of vegetation types (Jorgensen, 2011). Efforts, however, are not distributed equally across vegetation types. Although most biomes of the world are addressed in process-based modelling, models mostly focus on the dominant species group or growth form within these biomes, assuming that their dynamics are what drives the overall dynamics of the ecosystem. Most grassland and forest models, for example, focus exclusively on herbaceous plants and trees, respectively (Porté et al., 2002; Taubert et al., 2012). For some systems, such as savanna

71 ecosystems, where both woody vegetation and herbaceous plants are jointly determining ecosystem
72 dynamics, models already include multiple growth forms (e.g. Tietjen et al., 2016; Simioni et al., 2000).

73 In principle, the same holds for temperate forests, where understorey communities, including shrubs, herbs,
74 grasses and small trees, influence ecosystem dynamics through their effect on nutrient cycling and tree
75 regeneration (Gilliam, 2007). Nonetheless, understorey communities are frequently ignored in models of
76 temperate forest dynamics, possibly because their functional role remains widely underestimated (Gilliam,
77 2007). Consequently, efforts to model understorey dynamics have been scarce. The absence of models for
78 these communities makes it hard to predict their future response to global change and to estimate the
79 potential mediating role of the tree canopy (e.g. De Frenne et al., 2013; Verheyen et al., 2012). This extra
80 layer of complexity, literally, means that extrapolating results from models designed for other vegetation
81 types, such as grasslands, is not necessarily a valid solution. Given the fact that understorey communities
82 react to global change (e.g. Bernhardt-Römermann et al., 2015; De Frenne et al., 2015; Verheyen et al., 2012)
83 and play an important role in forest ecosystems (Gilliam, 2007), the inability to predict their future dynamics
84 constitutes an important research gap.

85 In this paper, we review fourteen published understorey models and consider their design in the context of
86 the processes required to predictively model the composition and structure of forest understoreys under
87 global change. We start with a description of the reviewed models in section 2. In section 3, we present a
88 conceptual model that catalogues variables and pathways that are deemed important to predict the impacts
89 of global change on forest understoreys. In section 4, we evaluate to what extent and in what way existing
90 models account for these variables and pathways. Finally, we outline how next generation models could
91 advance the state-of-the-art of forest understorey modelling.

92 **2. Review of understorey models**

93 Through a Web Of Science title search (search string: ("ground vegetation" OR understor* OR (forest AND
94 herb*)) AND (model* OR predict* OR simulat*)), we compiled an overview of studies modelling the dynamics
95 of understorey communities, published during the last three decades. This query resulted in a list of 132
96 publications in September 2017. Lit This set was subsequently amended by scanning reference lists for
97 additional relevant publications. This procedure led to the identification of 14 understorey models, each
98 described in one or more publications (Table 1). Although we focus on process-based models, most of these
99 models made use of empirical modelling techniques as well.

100
101

Table 1. Overview of published understorey models and their main characteristics, including model type, temporal and spatial grain, thematic focus, main drivers, link with the overstorey and rationale for model development. Model types are elucidated in the main text. NA indicates missing information.

Reference	Model type	Temporal grain	Spatial grain	Thematic representation of the understorey	Understorey drivers	Overstorey drivers	Overstorey representation	Model aim
Kellomäki and Väisänen (1991)	Logistic growth curves	1 year*	100 m ² *	Biomass of three PFTs (pioneer, intermediate and climax species)	Overstorey, Soil	Climate, N deposition, forest management	Individual-based tree growth model	Methodological advances
Nabuurs (1996)	Logistic growth curves	1 month	400 m ²	Biomass of seven understorey species (<i>Agrotis capillaris</i> , <i>Calluna vulgaris</i> , <i>Deschampsia flexuosa</i> , <i>Molina Caerulea</i> , <i>Pteridium aquilinum</i> , <i>Vaccinium myrtillus</i> , <i>Vaccinium vitis-idaea</i>)	Overstorey	NA	NA	Habitat modelling
Kupferschmid and Bugmann (2005)	Rule-based model	1 year	< 1 m ²	Cover of 25 microsite types	Overstorey	Natural disturbance, understorey	Rule-based model	Overstorey regeneration
Muukkonen and Mäkipää (2006)	Empirical model	1 year	2 m ² ***	Biomass of four groups (dwarf shrubs, herbs and grasses, mosses and lichens)	Overstorey, soil, climate	NA	NA	Predicting carbon budgets
Khanina et al. (2007)	Rule-based model	1 year	NA	Species presence/absence of six plant communities	Overstorey, soil	Climate, forest management	Individual-based tree growth model	Predicting understorey composition
Vospernik et al. (2007)	Empirical model	5 year**	707 m ² ***	Cover of nine vegetation classes (graminoids, ferns, herbs, <i>Vaccinium spp</i> , <i>Rubus spp</i> , ferns, shrubs, deciduous trees and conifers)	Overstorey, soil	Forest management	Individual-based tree growth model	Habitat modelling
Winkler and Heinken (2007)	Demographic model	1 year	25 cm ²	Number of individuals of single species (<i>Melampyrum pratense</i>)	Climate	NA	NA	Understanding understorey dynamics
Popovic and Lindquist (2010)	Physiological model	1 day	Individual plants	Biomass of two species (<i>Scilla bifolia</i> , <i>Arum maculatum</i>)	Overstorey, climate	NA	NA	Methodological advances
Belyazid et al. (2011)	Semi-empirical	1 month	1 m ²	Cover of five indicator species (<i>Sphagnum mosses</i> , <i>Vaccinium myrtillus</i> , <i>Deschampsia flexuosa</i> , <i>Blechnum spicant</i> , <i>Origanum vulgare</i>)	Overstorey, soil	Climate, Forest management, N deposition	Biogeochemical tree growth model	Predicting understorey composition
Matejcek et al. (2011)	Differential equation model	Continuous time	1 m ²	Density of four species (<i>Avanella flexuosa</i> , <i>Calamagrostis villosa</i> , <i>Vaccinium myrtillus</i> and <i>Picea abies seedlings</i>)	Overstorey, soil, topography	NA	Static	Overstorey regeneration

Dahlgren and Ehrlén (2012)	Demographic model	1 year	25 m ²	Number of individuals of single species (<i>Actaea spicata</i>)	Soil	NA	NA	Understanding understorey dynamics
Meen et al. (2012)	Empirical model	1 year	Individual plants	Indicators of plant performance for a single species (<i>Cornus suecica</i>)	Overstorey, soil	Climate	Individual-based tree growth model	Methodological advances
Thrippleton et al. (2016)	Logistic growth curves	1 year	625 m ²	Biomass of five PFTs: grasses, tall forbs, small herbs, ferns and shrubs	Overstorey, soil, climate	Climate, natural disturbance, understorey	Individual-based tree growth model	Overstorey regeneration
Thom et al. (2017)	Empirical model	1 year	625 m ² ***	Vascular plant species richness up to 60 cm in height	Overstorey, climate	Climate, natural disturbance	Individual-based tree growth model	Predicting understorey composition

102 * Information retrieved from Botkin et al. (1972)

103 ** Information retrieved from Monserud and Sterba (1996)

104 *** Corresponds to the plot size used for gathering data in the field

105 Our review of the literature illustrates that modelling understorey communities and how they develop over
106 time has been a topic of interest for at least 25 years. However, modelling attempts are relatively scarce
107 when contrasted with the high number of empirical studies, including both experimental (e.g. De Frenne et
108 al., 2015; Maes et al., 2014) and resurvey studies (e.g. Amatangelo et al., 2011; Bernhardt-Römermann et al.,
109 2015; Li and Waller, 2015; Verheyen et al., 2012;), carried out within this research domain.

110 Although most models documented in the literature were developed independently, many similarities
111 between underlying modelling concepts can be identified (Table 1). Based on these similarities, models can
112 be subdivided into four broad categories: (1) models based on logistic growth curves, (2) rule-based models,
113 (3) demographic models and (4) empirical models. Although we only label the last category as empirical,
114 many of the reviewed models were to some extent based on empiricism. In our categorization, we define
115 empirical models as models that relate system responses to system inputs without any prior information
116 concerning underlying processes or shapes of the equations to be fitted.

117 The first set of models simulate the mass of one or more understorey species or species groups based on
118 logistic growth functions parameterized with two static parameters: maximum biomass and maximum
119 growth rate (see, for example, Thrippleton et al., 2016). Correction factors are used to account for resource
120 limitations, more specifically, for light limitation (Nabuurs, 1996; Thrippleton et al., 2016) and nutrient
121 limitation (Kellomäki and Väisänen, 1991). The availability of these resources can be derived from the
122 characteristics of the overstorey, dynamically approximated by tree growth models.

123 Rule-based models, on the other hand, characterize the dynamics of the understorey based on a set of static
124 if-then rules: "If the current vegetation type at time t is x , then it will change to vegetation type y at time
125 $t+1$ ". Rules can be either deterministic (Khanina et al., 2007) or probabilistic, e.g., integrated into first order
126 Markov chain models (Kupferschmid and Bugmann, 2005). The if-clause can either depend on the previous
127 state of the vegetation only (Kupferschmid and Bugmann, 2005), hence assuming a predetermined
128 successional pathway, or can take additional environmental variables into account to dynamically simulate
129 shifts in vegetation composition (Khanina et al., 2007).

130 Demographic models mainly focus on species' life cycles, modelling reproduction rates, numbers of offspring,
131 and seed dispersal (e.g. Meen et al., 2012). Current approaches documented in the literature are limited to
132 modelling the spatial distribution and density of single species (Dahlgren and Ehrlén, 2012; Winkler and
133 Heinken, 2007). Both reviewed studies derived demographic rates from site-specific measurements and did
134 not include competition processes. Therefore, their models can't be expanded towards other systems,
135 especially those wherein multiple species interact.

136 A final group of models consists of empirical approaches. In these models, relationships between overstorey
137 structure and species composition in the understorey are statically defined, based on empirical data. As a
138 result, understorey changes only occur following a change in the overstorey. Other studies dealt with this

139 limitation by considering forest age (Muukkonen and Mäkipää, 2006) or environmental conditions as
140 additional predictors (Thom et al., 2017; Vospernik et al., 2007). In the latter models, predictions of
141 understorey composition can change from year to year, regardless of whether overstorey changes occur.

142 In addition to these four broad groups of models three other unique modelling approaches have been
143 proposed. Popovic and Lindquist (2010) applied a physiological model, initially developed for crop yield
144 modelling, that explicitly accounts for below- and above-ground competition, and models growth primarily
145 based on photosynthetic rates. Matejcek et al. (2011) used a discrete space, continuous time differential
146 equation model, inspired by diffusion models in physics, to determine the spatial spread of understorey
147 species taking into account a range of environmental factors. A final approach, developed by Belyazid et al.
148 (2011), makes use of response functions, which represent the response of individual species to a range of
149 environmental factors, not taking into account competition with other understorey species. By comparing
150 species-level responses derived from these response curves the available space is distributed among all
151 competing species. To account for time lags, an additional parameter, inversely related to a species' lifespan,
152 is included.

153 The temporal resolution of the reviewed models is, apart from some exceptions (Matejcek et al., 2011;
154 Popovic and Lindquist, 2010), widely congruent. Timesteps were generally set to one year, i.e., a single
155 growing season. The popularity of this timestep is most likely related to the popularity of one-year-timesteps
156 in tree growth models (Bugmann, 2001). Model coupling is facilitated considerably by applying the same
157 timestep for understorey and overstorey growth. Similarly, but less frequently, spatial resolution is
158 determined by the overstorey models used, with grains typically ranging between 25 and 1000 m² (e.g.
159 Nabuurs, 1996; Thrippleton et al., 2016). Within these grid cells, models assume uniform abiotic conditions
160 and, consequently, a uniform understorey composition. Less than half of the reviewed models focused on
161 individual plants, or opted for smaller grain sizes of approximately 1 m².

162 The level of detail of the model output, also referred to as the model's thematic resolution, was again largely
163 comparable among models. The reviewed models either simulated the dynamics of a single species, multiple
164 species or a limited set of species groups, referred to as plant functional types (PFTs). These differences were
165 largely explained by the aim of the model. Single species models aimed at understanding a species'
166 population dynamics (Dahlgren and Ehrlén, 2012; Winkler and Heinken, 2007), while multiple species models
167 or PFT-based models aimed at predicting community composition, either in terms of indicator species
168 (Belyazid et al., 2011) or in terms of a community's functional characteristics (Muukkonen and Mäkipää,
169 2006; Thrippleton et al., 2016; Vospernik et al., 2007). Species or species groups were either represented in
170 terms of numbers of individuals or in terms of biomass. Modelled species include either indicator species or
171 functionally important species, i.e. species that are expected to influence overstorey regeneration, such as
172 *Pteridium aquilium*, *Deschampsia flexuosa*, *Vaccinium spp* and *Rubus spp* (e.g. Fotelli et al., 2002; Harmer and
173 Morgan, 2007; Petriřan et al., 2012; Parker et al., 2009).

174 Overall, we found substantial variation among existing understorey models in terms of model concepts and
175 the level of detail taken into account. Although differences among models can often be attributed to
176 differences in research objectives, this was not generally the case for the reviewed understorey models.
177 Different objectives were tackled with similar modelling approaches and vice versa. In general, understorey
178 modelling was either driven by the need to appraise the influence of understorey growth on overstorey
179 regeneration (Kupferschmid and Bugmann, 2005; Matejicek et al., 2011; Thrippleton et al., 2016), to
180 understand understorey community assembly or population dynamics (e.g. Winkler and Heinken, 2007), to
181 predict forage supply over time (e.g. Nabuurs et al., 1996) or to predict understorey diversity (e.g. Thom et
182 al., 2017).

183 **3. A process-based perspective on forest understorey dynamics**

184 Nearly all of the models documented in the literature are based on simplified mathematical concepts that
185 are successful in reproducing patterns of understorey dynamics for the case studies under investigation. It
186 remains questionable, however, whether their results can be extrapolated to new environmental conditions
187 and whether they can predict alternative properties of understory communities, such as, community trait
188 values and distributions. These features are of crucial importance when effects of global change on the
189 understorey are to be identified in terms of composition, structure and functioning. For this purpose, more
190 process-based approaches are needed.

191 Although such models have already been proposed for other vegetation types (Jørgensen et al., 2011), they
192 might not be readily applicable for understoreys. While the dynamics of understorey species and their
193 communities are driven by similar ecological processes as those observed in other vegetation types (e.g.
194 growth, mortality, competition), resources and conditions that support these processes differ considerably
195 in a forest compared to, for instance, a grassland system. Instead of being driven primarily by climate (e.g.
196 irradiation, annual mean temperature, precipitation), soil conditions (e.g. nutrient content, water availability)
197 and neighbouring competitors, resources and conditions for understorey plants are filtered by the forest
198 environment (Figure 1), leading to altered resource levels and dynamics, potentially requiring different
199 modelling routines to account for them.

200 Below we discuss how the forest environment affects resources and conditions for understorey growth,
201 focussing on those aspects that are characteristic for the forest environment: the presence of an overstorey,
202 a litter layer, tree roots, disturbances with varying frequency and severity and potential legacies of past
203 (agricultural) land use. We focus here on temperate deciduous forests, dominated by tree species that shed
204 their leaves during winter, giving rise to a dynamic light environment throughout the year. The litter layer in
205 these forests consists predominantly of quickly decomposing leaves and woody debris. Water is abundantly
206 available and soils are relatively fertile due to the yearly supply of organic matter. In these forests, 80 to 90

207 % of plant biodiversity is concentrated in the understorey, consisting of herbs, grasses, shrubs and tree
 208 seedlings (Gilliam, 2007).

209
 210 **Figure 1.** Schematic overview of the most important mechanisms that influence understorey community dynamics in temperate
 211 forests, with a focus on mechanisms that act at the local scale. Landscape influences were not included.

212 3.1. The canopy layer

213 The tree canopy and its impact on light availability is probably one of the most studied factors in forest
 214 ecology, specifically in relation to tree regeneration (Lieffers et al., 1999). The canopy layer modifies light
 215 that reaches the forest floor in two ways: (1) the canopy lowers the amount of light, and hence modifies the
 216 pattern of light availability, and (2) it changes the ratio between the red and infrared spectrum of the light,
 217 also referred to as the quality of light.

218 Due to the phenological cycles of the overstorey, light availability and quality vary throughout the year. These
 219 phenological cycles have given rise to the adoption of contrasting strategies by forest understorey species,
 220 ranging from light-demanding species that fulfil their life cycle before tree budburst in spring to shade-
 221 tolerant species that are able to grow in a low light environment during the rest of the growing season. These
 222 differences in temporal niches are an important mechanism explaining species co-occurrence in understorey
 223 communities (Bratton, 1976). In the light of climate change, which is expected to modify seasonal patterns
 224 of temperature and precipitation (IPCC, 2014) as well as impact phenological processes, also strategy-specific
 225 responses of forest understorey species can be expected due to shifting temporal niches. In addition to

seasonal light dynamics the canopy further modifies diurnal light dynamics. In a closed forest, only a small fraction of total daily irradiation reaches the forest floor, predominantly as diffuse light. During several short periods, also direct irradiation reaches the forest floor. These so-called sun flecks are generally scarce, but often responsible for a large portion of the total amount of light that reaches the forest floor and, hence, for a large share of carbon that is assimilated by the understorey (Chazdon and Pearcy, 1991; Way and Pearcy, 2012). This share, however, depends on the number and the size of sun flecks which, in turn, depend on the canopy structure. Many small sun flecks, for example, are assumed less important for understorey growth than one large sun fleck (Lieffers et al., 1999). Although the influence of canopy structure on the partitioning between direct and diffuse irradiation has been studied, it has rarely been included in process-based vegetation models (Way and Pearcy, 2012).

Light quality, on the other hand, refers to the ratio between the red and far red spectrum of light. After overstorey leaf flushing, this ratio is lowered from 1.2 (equivalent to open field conditions) to around 0.2 at the forest floor, a value which varies with overstorey tree species composition (Daws et al., 2002; Vazquez-Yanes et al., 1990). As germination is known to be highly dependent on light quality (Jankowska-Blaszczuk and Daws, 2007), changes in overstorey composition might result in altered germination patterns.

The canopy also influences nutrient availability. In addition to transferring nutrients from the mineral soil to the topsoil via leaf litter production (a process referred to as 'nutrient pump' in Figure 1), the canopy also modifies the input of atmospheric components, which is especially true for nitrogen (e.g. Avila et al., 2017; Fowler et al., 1989). De Schrijver et al. (2007), for example, found that coniferous canopies transfer on average 1.7-times more NO_3^- and NH_4^+ to the soil than deciduous canopies. This may increase nitrogen availability for the understorey but can also increase soil acidification (De Schrijver et al., 2012) which, in turn, can affect nutrient and base cation availability as well as the availability of aluminium, an element which is toxic for many plant species (Falkengren-Grerup et al., 1995).

The canopy lowers overall water availability by reducing throughfall and alters the distribution of precipitation within a stand, as stemflow concentrates precipitation in the zones surrounding the stems (Staelens et al., 2008, 2006). This is particularly true for tree species with a smooth bark and branches angled upwards, such as European beech (*Fagus sylvatica* L.). Partitioning between interception, throughfall and stemflow depends on rainfall characteristics, but also on tree species, successional status of the forest, and stand density (Barbier et al., 2009). Deciduous canopies also modify the temporal pattern of incoming precipitation during the year, reducing water availability more strongly during the growing season. This might, for example, lead to an increased impacts of summer droughts as temperature and evaporation rates rise due to climate change (IPCC, 2014). Hence, both climate change and changes in overstorey composition can result in changes in water availability at the forest floor.

259 The canopy layer also determines the forest microclimate to a large extent (Barkman, 1992), leading to lower
260 temperatures and reduced wind speed, which are both lowering evaporation rates at the forest floor. Both,
261 the species composition of the overstorey (Porté et al., 2004) and the closure of the canopy (De Frenne et
262 al., 2013) influence the magnitude of this microclimate effect, which can influence water use efficiency and
263 growth of understorey plants. As shown by De Frenne et al. (2013), it is important to include this climate
264 buffering capacity of the overstorey for predicting development trajectories of forest understoreys.

265 3.2. The litter layer

266 Similar to the canopy, litter modifies the quantity and quality of light available for seeds embedded in or
267 below the litter layer (Vazquez-Yanes et al., 1990). Hence, changes in litter dynamics, such as increased
268 decomposition due to overstorey disturbance or climate change, might promote the germination of more
269 light demanding species, again altering understorey germination patterns.

270 In temperate forests, the quality of leaf litter produced by the overstorey strongly influences nutrient
271 availability. The total mass of leaf litter and its decomposability both significantly influence the amount of
272 nutrients available for the understorey. As shown by Augusto et al. (2003), the decomposition process
273 predominantly influences the nutrient content of the top layer of the soil, coinciding with the rooting depth
274 of most understorey species.

275 Leaf litter can also produce organic acids during decomposition (Nilsson et al., 1982). Together with the
276 efficiency of the overstorey to capture acidifying components (see section 3.1), litter quality is considered
277 one of the main driving factors of soil acidification by the overstorey (De Schrijver et al., 2012), and need to
278 be taken into account in process-based models of forest understorey dynamics.

279 Leaf litter can have a direct negative effect on understorey growth as it can produce chemical components
280 that inhibit understorey growth, generally referred to as allelopathy (Barbier et al., 2008). Tree species
281 composition of the overstorey as well as an understorey species' susceptibility to allelopathic compounds
282 determine whether growth inhibition through allelopathy needs to be taken into account in modelling
283 understorey growth. Next to chemical inhibition, litter may also inhibit understorey growth mechanically. As
284 most seedlings are only able to establish if their roots reach the mineral soil, a thick litter layer may inhibit
285 establishment, mainly for seeds that germinate on top of the litter layer. For seeds that germinate below the
286 litter layer, the ability of the shoot to penetrate the litter layer is crucial for establishment.

287 Next to these inhibiting effects of litter, the litter layer can also promote establishment, as it conserves soil
288 moisture (Albrecht and McCarthy, 2009; Facelli and Pickett, 1991). Hence, litter may have positive or negative
289 effects on establishment, depending on the environmental conditions and the thickness of the litter layer
290 (Xiong and Nilsson, 1999). Litter, such as coarse woody material, can also act as a substrate itself, promoting
291 the growth of species specifically adapted to these substrate types (e.g. Kumar et al., 2017).

3.3. The root layer

Trees take up nutrients and water via their root system. Therefore, the presence of tree roots close to the soil surface may lead to competition for nutrients and water with the understorey (Barbier et al., 2008). As tree species differ in root morphology and the vertical distribution of fine roots (Gale and Grigal, 1987), competition for belowground water resources might differ among tree species. There are also seasonal differences in the amount of water extracted from the soil, depending on the photosynthetic activity of the overstorey. In addition, tree roots can also increase water and nutrient availability for the understorey. Some tree species can redistribute water from deep soil layers to drier top layers, generally referred to as hydraulic redistribution (Neumann and Cardon, 2012). Moreover, some tree species fix inorganic nitrogen from the atmosphere, which directly increases nitrogen availability for the understorey. However, this may also increase soil acidity by accelerating nitrification (Van Miegroet and Cole, 1984). Negative effect of soil acidification has been discussed in section 3.1.

A final factor which might influence the performance of understorey plants is the presence of mycorrhizal fungal communities (Uibopuu et al., 2012). As forest age and tree species composition influences mycorrhizal fungal community composition (Lang et al., 2011), this might be an additional pathway of overstorey – understorey interaction, worthy to be included in understorey models.

3.4. Forest disturbances and land use history

Harvesting activities, storm events, insect outbreaks and forest fires are considered as the most important disturbance events in forests (Seidl et al., 2011b). For understoreys, browsing can be additionally important (Roberts and Gilliam, 2003). Overstorey disturbances often lead to sudden increases of resource availability, resulting in germination of dormant seeds and/or accelerated understorey growth (Battles et al., 2001). Next to influencing resource availability, disturbances can also lead to mortality of understorey plants depending on the severity of the disturbance event and species-specific responses to disturbances (e.g. Abella and Springer, 2015; Zenner and Berger, 2008; Rooney and Waller, 2003). Especially when frequent disturbances occur, species-specific responses can play a dominant role in structuring emerging plant communities (Keith et al., 2007; Noble and Slatyer, 1980). As most forest herbs are perennial and only reach maturity after several years, disturbances can in some cases lead to local extinction of understorey species and are thus important to consider when predicting future understorey composition. When disturbance events have persistent negative effects, such as soil compaction after intensive harvest events (Ampoorter et al., 2012), elevated mortality rates may occur for a longer period of time.

Also past human disturbances, often referred to as a forest's land use history, can affect current resource levels and growing conditions at the forest floor, but also future development trajectories of understorey communities (Perring et al., 2016). Land use history determines, for example, the availability of phosphorus, with high levels of phosphorus in forests established on former agricultural soils with an extensive history of

326 fertilization (Flinn and Marks, 2007). The influence of phosphorus on community composition will depend on
327 the environmental conditions and the species under consideration (e.g. Baeten et al., 2009). Next to its
328 influence on phosphorus levels, land use history also determines the composition of the seed bank which will
329 determine community composition after major disturbances that promote germination of dormant seeds.

330 **4. Mechanistic foundation of existing understorey models**

331 As discussed above, the forest environment alters the resources and conditions at the forest floor via a
332 diverse set of pathways. These, in turn, affect multiple demographic processes of understorey plants. Here,
333 we assess to what extent and how current models account for these processes (Figure 2).

334 First of all, there is an imbalanced consideration of resources in existing understorey models. Most studies
335 focus solely on light, while a minority also accounts for water and nutrient limitations (e.g. Belyazid et al.,
336 2011). Studies that do take nutrient limitations into account largely focus on nitrogen availability or use more
337 general proxies, such as site quality indices. None of the reviewed models account for phosphorus limitations,
338 a crucial aspect especially when understorey trajectories in post-agricultural forest sites are considered
339 (Baeten et al., 2009). Similarly, effects of other environmental factors, including microclimate, soil acidity and
340 mycorrhizal fungal communities, are clearly underrepresented in current modelling initiatives.

341 Second, none of the reviewed models consider the litter layer explicitly. This contrasts with the empirical
342 evidence discussed above. Although it has been shown that the litter layer may affect demographic rates,
343 none of the reviewed models took these relationships explicitly into account.

344 There is also a clear divide between the reviewed models regarding the processes considered. Understorey
345 models either focus on competition and growth or on germination, establishment, reproduction and
346 mortality (See Figure S1 in Supporting Information). These differences in focal processes result in different
347 model concepts to be used. While the first group mainly considers dynamics in plant biomass, the second
348 group focusses on the number of individual plants.

349 When looking specifically at the drivers that are accounted for in predicting understorey dynamics, we
350 identified a clear trend. While most models consider the overstorey as one of the most important factors
351 directly determining understorey composition (predominantly through its influence on the light
352 environment), direct influences of global change drivers were considered less frequently. The impact of
353 global change was generally modelled via overstorey changes using a linear model chain, connecting
354 overstorey models to understorey models. First, overstorey dynamics are simulated in response to a series
355 of global change drivers. Next, understorey composition is predicted based on the simulated overstorey
356 which determines the growing conditions for the understorey. Although such a model chain is promising, the
357 way it has been put into practice might be suboptimal. Most of the time, only light is used to describe the
358 conditions at the forest floor, while other resources and conditions are frequently overlooked.

359

360 **Figure 2.** Schematic overview of modelled relationships in the reviewed understorey models. The term (sub)model target refers to
 361 processes or state variables that are explicitly predicted by a model or one of its submodels. A proxy refers to an indicator that
 362 characterizes multiple state variables at once (e.g. soil quality scores). For more details on individual models, we refer to the
 363 Supporting Information (Figure S1).

364 Although we classified most of the reviewed models as being process-based (because they explicitly model a
 365 range of processes), most of the processes they consider are modelled empirically. Growth modelling is, for
 366 example, often based on logistic response curves (e.g. Thrippleton et al., 2016). Similarly, demographic rates
 367 are usually estimated based on regression models with environmental conditions as predictor variables (e.g.
 368 Dahlgren and Ehrlén, 2011). These empirical approaches make extrapolating existing models to new
 369 environmental conditions or other species groups inappropriate.

370 5. Ways forward for modelling forest understorey

371 5.1. Dealing with complexity

372 In this review, we have highlighted empirical evidence for the influence of a variety of processes on
 373 understorey community composition in temperate forests, and document that only a minority of these
 374 processes are included in existing understorey models. This, however, does not necessarily mean that existing
 375 models cannot predict understorey composition reliably. Numerous vegetation models have shown that not
 376 all processes need to be included to achieve good predictive performance (e.g. Fontes et al., 2010). A process

377 that has been proven to influence understorey composition in a single factorial experiment, for example,
378 might appear irrelevant when other driving processes are considered as well. Including such a process will
379 not improve model performance. Instead, it will only increase the complexity of the model and the amount
380 of parameters to be estimated. Therefore, models aim at including only the most important processes, i.e.
381 those that are able to influence the system's characteristics of interest.

382 However, defining the processes that play a dominant role is challenging. While in some cases, one can rely
383 on experts in the field, most of the time inspiration is drawn from existing models and the processes they
384 consider. Most of the reviewed understorey models, for example, were based on modelling concepts that
385 have proven to be successful for other vegetation types. The processes, accounted for by these models,
386 however, are those that are important for the vegetation type they were originally developed for. Although
387 this strategy can be successful by altering the relative importance of the included processes (see, for example,
388 Taubert et al., 2012), we argue that this is a suboptimal approach for understorey modelling, as it might lead
389 to the omission of potentially important processes in understorey dynamics. Furthermore, it is suboptimal
390 because environmental conditions at the forest floor (and their temporal dynamics) aren't comparable to
391 those experienced by other vegetation types. This means the processes and/or the way they need to be
392 modelled might deviate considerably from those included in existing models for other vegetation types such
393 as forest overstorey or grasslands.

394 Process-based models can help in identifying the most important processes determining understorey
395 dynamics. As a first step, one needs to develop a process-based model that considers those processes that
396 are deemed important based on empirical evidence (as described in section 3). Here, special attention needs
397 to be paid to integrating demographic and physiological processes (Jeltsch et al., 2008). Next, by sensitivity
398 analyses or by comparing model runs that either include or exclude a specific process, the relative importance
399 of individual processes and associated parameters can be revealed. Subsequently, model calibration can
400 focus on these critical processes and parameters, in order to improve model performance.

401 5.2. From PFT-based to trait-based approaches

402 Modelling changes in community composition involves modelling individual species and changes in their
403 relative abundance. Modelling the entire available species pool of forest understorey plants, however, might
404 be unrealistic. Modellers have overcome this problem by modelling a range of plant functional types (PFTs)
405 that represent the different strategies that occur in the available species pool (Cramer, 1997). One of the
406 main limitations of using PFTs is that at least some strategies that exist in reality will be ignored (Van
407 Bodegom et al., 2012). This is especially problematic for highly diverse understorey communities that harbour
408 a broad range of strategies. Although this issue can be partially addressed by increasing the number of PFTs,
409 this is rarely done as each additional PFT requires a new set of parameters (or even equations) that determine

410 its response to the environment. As these parameters are generally derived empirically, increasing the
411 number of PFTs drastically increases data needs.

412 Alternatively, one can model a PFT's response in a more mechanistic way, by explicitly considering the
413 mechanistic links between plant functional traits and demographic rates, jointly determining its response to
414 the environment (Suding et al., 2008). These plant functional traits are broadly defined, ranging from traits
415 that determine a plant's architecture (e.g. specific leaf area, height), its tissue's chemical composition (e.g.
416 leaf nitrogen content) and its physiological rates (e.g. photosynthetic efficiency) (Violle et al., 2007). In a
417 modelling context, these traits can be used to estimate a broad range of process rates (e.g. growth, dispersal
418 ability, water use) and, hence, the way a PFT will respond to its environment. The main advantage of this
419 trait-based approach is that adding a PFT only requires additional trait values, not extra equations or
420 parameters describing growth and demographics. Realistic combination of trait values can be generated
421 automatically (e.g. Pappas et al., 2016), based on measured trait values in the field, their frequency
422 distributions and correlation structures among them (Diaz et al., 2016; Wright et al., 2004), giving rise to the
423 possibility to increase the number of PFTs considerably. Although we believe that simulations with fixed PFTs
424 are still useful and sometimes the only feasible method to predict responses to global change (e.g. some
425 processes might still require empirical response functions), we advocate implementing mechanistic links
426 between traits and species performance to facilitate upscaling to a larger set of PFTs. Additionally, the
427 outputs generated by trait-based modelling, which can be expressed in terms of community weighted mean
428 trait values and trait ranges, will be better proxies to express the functioning of the understorey and its
429 species richness (Lavorel and Garnier, 2002), compared to those generated by PFT-based modelling.

430 Next to grouping plant species on a functional basis, one also needs to decide how to group individuals within
431 a specific functional group. Several strategies exist to address this issue. One can either consider all individual
432 plants independently (individual-based modelling), group individuals with identical behaviour to increase
433 computational efficiency (cohort-based modelling), or simply merge all individuals of a specific functional
434 group. Cases where individual-based modelling is preferred are those where a limited number of clearly
435 recognizable individuals need to be modelled. As this is generally not the case for understorey modelling,
436 individual-based approaches might become computationally intractable. This was confirmed by the reviewed
437 models, where individual-based approaches were only used for single species modelling (e.g. Winkler and
438 Heinken, 2007). Cohort-based approaches group individuals based on similar behaviour. In most cases, size
439 classes are used, as these largely determine an individual's competitive performance and growth rate. As
440 intraspecific size differences in understorey communities are rather small, compared to those found in
441 overstorey communities (Bugmann et al., 2001), grouping based on size might be less relevant for this
442 vegetation type. However, also merging all individuals within one functional group is often not preferable.
443 As many understorey plants change their behaviour with age (Bierzychudek, 1982), age-classes might be
444 more relevant. Flowering, seed production and carbon allocation to reserve pools, for example, may depend

on plant age (Noble and Slatyer, 1980). Hence, we suggest that cohort-based modelling based on age classes could be a promising way to consider when modelling understorey dynamics.

5.3. Spatial and temporal resolution

In general, the desired spatial and temporal resolution for models varies depending on the question at hand. However, available options are constrained by the vegetation type of interest. As discussed above, the vegetation period of understorey species may differ from one species to the next. While some species try to fulfil their yearly life cycle before overstorey leaf flush, others are present the year round. These differences in temporal niches mean that the strength of competition between two species likely depends on the day of the year. To be able to explicitly consider these temporal niches, either subannual timesteps or elaborate upscaling procedures need to be used (Harvey, 2000).

The spatial grain of vegetation models is often set to the area wherein individuals are expected to compete for the same resources. Within this area, resources and conditions are assumed to be uniform and locations of individual plants are generally not specified. This simplification, as applied in forest gap models, reduces the complexity of numerical calculations considerably compared to models that calculate competitive interactions spatially explicitly, based on the geographical location of competing individuals and their zones of competitive influence (e.g. Reineking et al., 2006). For understorey modelling a similar approach can be applied. Grain sizes, however, will need to be a lot smaller than those used in forest gap models, preferably ranging between several dozen square centimetres to one square metre. When defining grain sizes for vegetation models, one also needs to consider the spatial heterogeneity of resources and conditions. As this heterogeneity is an important factor that may explain species co-existence (Kumar and Chen, 2017; Tilman, 1982), grain sizes should be able to capture this heterogeneity in order to avoid underestimating diversity on a larger scale. As discussed in section 3, the forest environment not only modifies resource levels but can also increase their spatial heterogeneity, suggesting the need for small grain sizes.

5.4. Predicting responses to global change

The next generation of process-based understorey models should be able to predict understorey responses to changes in resources and conditions at the forest floor. Our suggestions above will aid this endeavour. However, the way global change translates to changes in environmental conditions at the forest floor will critically depend on overstorey states and dynamics. The forest overstorey can mediate the impact of global change on understorey diversity and functioning via a broad range of pathways (section 3, Figure 1). Although many of these pathways have the potential to dampen the impacts of global change, others also hold the potential to amplify them. Litter accumulation can, for example, mediate the impact of drought, but can also amplify soil acidification. Whether specific processes will amplify or dampen the impacts of global change will depend on the environmental context, the species considered, and the timeframe of interest.

478 Process-based understorey models have the potential to investigate these complex interactions. As a first
 479 step, these models can be used to investigate how understorey communities respond to changes in resources
 480 and conditions at the forest floor without explicitly modelling the overstorey. Such simulations can provide
 481 information on potential interactions among the local drivers of community composition, such as nutrient
 482 availability, water availability, light availability and temperature. Using this approach to assess the impact of
 483 a specific global change scenario requires selecting trajectories of local drivers that are representative for
 484 this global change scenario. This task, however, is far from straightforward. To be able to predict such
 485 trajectories one needs to know how global change drivers, often expressed at the regional level, affect the
 486 overstorey and how global change together with the overstorey affects the microclimatic conditions and soil
 487 characteristics, determining the growing conditions for the understorey. Such predictions can be made by
 488 coupling atmospheric models, forest dynamic models and micro-climate models in a hierarchical manner,
 489 going from regional changes (climate, acidifying deposition) and stand-level changes (overstorey response to
 490 climate change, alternative forest management) to changes in local growing conditions for understorey
 491 plants. Coupling this model chain to process-based understorey models can be seen as the next step to
 492 predict understorey responses to global change. Subsequently, feedbacks can be added to the model chain,
 493 including altered tree regeneration rates through competition between understorey plants and tree
 494 seedlings, and soil quality changes through uptake and release of nutrients by the understorey (see also
 495 Kupferschmid and Bugmann, 2005; Thrippleton et al., 2016). Modelling these feedbacks will likely improve
 496 predictions and provide valuable information on the functional role of the understorey and its importance
 497 for long-term forest growth.

Influence of...	Climate	N deposition	Management	Tree species	Litter layer	Light	Water	Nitrogen	Phosphorous	Base cations	Soil pH	Microclimate	Mycorrhiza	Germination	Establishment	Growth	Mortality	Reproduction	Abundance	Composition
on...																				
Climate	1																			
N deposition		1																		
Management			1																	
Species composition	5	3	5	1																2
Density	5	3	4	1																2
Litter layer	1	1	1		1															
Light				3	3	1														
Water	1			2	2		1													
Nitrogen		2		2	2	1		1												
Phosphorous								1												
Base cations				1	1	1			1											
Soil pH	1	1		1	1	1				1										
Microclimate											1									
Mycorrhiza												1								
Germination													1							
Establishment														1						
Growth	2				2	4	1	1	1						1					
Mortality																1				
Reproduction	1				1												1			
Abundance	1			2	2	1	1	1		1	1			2	2	5	2	2		
Composition				2	1	1													7	

499 **Figure 3.** Overview of mechanisms accounted for by the reviewed models. Numbers refer to the number of publications that account
500 for the influence of factor x (column header) on factor y (row header). White grid cells represent top-down interactions, while grey
501 cells refer to bottom-up or feedback mechanisms.

502 Although some of the reviewed models already combine understorey models with soil and overstorey models
503 to investigate the impact of global change on understorey dynamics, many relationships in this complex
504 process chain have not yet been accounted for in models (Figure 3). Especially the absence of microclimate
505 models can be considered as an important missing link in such a linked modelling framework. Such missing
506 links highlight that in addition to advances in process-based understorey modelling, advances in other
507 research domain are needed to be able to predict the influence of global change on understorey dynamics.

508 5.5. Data needs

509 In order to develop the next generation of process-based understorey models, the availability of reliable data
510 is crucial. Although data on plant functional traits are becoming increasingly available via online databases
511 (e.g. www.try-db.org), not all traits and species are equally represented (Kattge et al., 2011). While forest
512 overstorey species are well-represented, additional efforts are needed to expand available data on
513 understorey species. Also data on traits that are hard to measure, such as root characteristics, are still scarce
514 (Kattge et al., 2011). In addition to data on individual traits, relationships among traits need to be further
515 investigated, while mechanistic links between traits and process rates need to be demonstrated and
516 measured (see section 5.3). Such data can be gathered via detailed measurements in growth experiments.
517 Finally, data on long-term changes in understorey community composition are needed. These data can be
518 used for model validation, but also for estimating parameter values that can't be measured in the field
519 directly. Such data are being gathered in permanent and quasi-permanent monitoring plots across Europe
520 and North America (see, for example, Verheyen et al., 2012). Long-term global change experiments, focussed
521 on understorey communities, can complement these observational data to attain more representative
522 calibration and validation data sets.

523 Clearly, process-based modelling of understorey communities will involve combining numerous different
524 data sets. As all these data sets come with their own levels of uncertainty, advanced techniques such as
525 Bayesian data assimilation (Clark, 2005) will be needed to account for these uncertainties when assimilating
526 data into models. This technique will also enable propagating uncertainties through the model, in order to
527 obtain an idea on how data uncertainty affects model output uncertainty.

528 6. Conclusions

529 Global change is altering the composition of the understorey in temperate forests. Although models have the
530 potential to increase our understanding of the mechanisms that drive these changes and can support the
531 development of mitigation strategies, only a small set understorey models are currently available. The
532 parsimony of these models contrasts with the complexity of the effects of global change described in the

533 literature. While most approaches succeed in modelling the impact of one or more global change drivers on
534 at least one community assembly process, none of them adopts a fully integrative approach, which would
535 enable us to assess the (interactive) effects of multiple global change drivers on the composition, structure
536 and functioning of the understorey. We contend that such an integration can be achieved by modelling the
537 dynamics of individual species and interactions among them in a more process- and trait-based manner. One
538 way to start this model development process is by focussing on those processes that have been found to
539 influence understorey community development. Next, through simulation and sensitivity analyses,
540 complexity can be reduced before data-based calibration takes place on retained, critical processes and
541 parameters. To be able to predict the understorey's response to global change, special attention needs to be
542 paid to the overstorey, which has the potential to modulate the effects of global change. Hierarchical
543 modelling, combining overstorey models and understorey models, should be considered to deal with this
544 extra layer of complexity.

545 **7. Declaration of interest**

546 The authors declare that they have no conflict of interest.

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