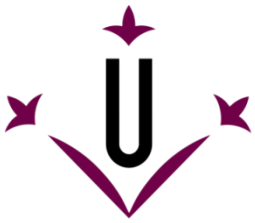

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Tree light capture and spatial variability of understory light increase with species mixing and tree size heterogeneity

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Abstract

Mixed and multi-layered forest ecosystems are sometimes more productive than monospecific and single-layered ones. It has been suggested that trees of different species and sizes occupy complementary positions in space which would act as a mechanism to increase canopy light interception and wood production. However, greater canopy light interception reduces the average amount and variability of transmitted radiation offering fewer opportunities for all species to regenerate and to maintain forest heterogeneity in the long-run. We investigated whether increasing overstory heterogeneity indeed results in greater canopy light interception and lower variability in transmittance. We modeled the three-dimensional structure of forest stands with 3 typical forest structures, 10 mixtures of four tree species, and 3 different basal areas. We used the forest light interception model SAMSARALIGHT and performed three-way analyses of covariance to analyze the effects of the three varied components of forest heterogeneity. We found no evidence that increasing structural heterogeneity increases canopy light interception. However, the light interception by mixed canopies was greater than the weighted average of light interception by the corresponding pure canopies. Variability in transmittance increased in some cases with compositional heterogeneity and, to a lesser extent, with tree size inequalities. The advantage of heterogeneous forests is in opportunities for natural regeneration as well as in opportunities to enhance canopy light interception.

Keywords

Understory light; tree species diversity; radiative transfer model; SAMSARALIGHT; forest structure

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Introduction

It has been advocated that forests with many tree species and a great heterogeneity in tree sizes are more productive (Pretzsch and Schütze 2009; Toïgo et al. 2015; Vallet and Pérot 2011), resistant and resilient (Jactel et al. 2005) to future changes and harbor a greater biodiversity (Huston 1979) than monospecific forests in which all trees have a similar size. Over the last 50 to 100 years, humans have applied forest management systems over much of the northern hemisphere that tended to simplify both the structure and composition of many forests (Bengtsson et al. 2000). This simplification resulted in increased production of the targeted product, usually timber of few species highly valued by the market at the time. However, the advantages of these management systems may have obscured long term negative impacts such as reductions of genetic and species diversity (Ledig 1992; Noss 1999), rigidity in the face of market and climate variations (Pretzsch et al. 2013), a decrease in forest habitat quality (Franklin et al. 2000) and soil fertility (Reich et al. 2012) and a loss in overall productivity. Many researchers and forest managers now promote the development of more heterogeneous forests (McElhinny et al. 2005; Puettmann et al. 2009), but our understanding of the sharing and use of resources among species and vegetation strata in heterogeneous forests is limited and impedes our ability to predict the long-term dynamics of such forests.

Researchers have usually hypothesized that forest productivity is greater in mixed forests than in the corresponding pure forests because species mixtures should capture more resources, and in particular, more solar radiation due to the layering of the forest canopy and the complementarity and overlapping of tree crowns (Bauhus and Schmerbeck 2010; Forrester et al. 2006; Kelty 2006; Pretzsch and Schütze 2009; Vallet and Pérot 2011; Yachi and Loreau 2007). It is also generally assumed that the structural and compositional heterogeneity of the forest overstory directly affects the amount and variability of light available in the understory for tree regeneration (e.g. Kelty 2006). A number of studies have found close relationships between the amount of light transmitted to the

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69 understory and canopy density (Comeau and Heineman 2003; Lochhead and Comeau 2012; Sonohat
70 et al. 2004; Vales and Bunnell 1988), stem spatial distribution (i.e. clumped, random or dispersed)
71 (Beaudet et al. 2011; Coates et al. 2003; Drever and Lertzman 2003; Ligot et al. 2014a; Lochhead and
72 Comeau 2012), vertical canopy structure or distribution of tree sizes (Drever and Lertzman 2003;
73 Ligot et al. 2014a; Lochhead and Comeau 2012), and species composition (Lochhead and Comeau
74 2012; Messier et al. 1998). The effects of these factors on understory light have been tested
75 individually and sometimes in pairs, but their combined effects have been particularly difficult to
76 assess.

77 Moreover, most studies have focused on the average quantity of light that reaches the forest
78 floor but few have considered spatial variability in light conditions (Puerta-Piñero et al. 2007) even
79 though it is also essential for the sustainability of structurally complex forests. Uneven-aged stands
80 harboring trees of different sizes and ages can only persist if sufficient light reaches seedlings at least
81 in scattered patches in the forest understory. Furthermore, the coexistence of different tree species
82 can only be ensured if the variability in understory light is sufficient for all species to be able to
83 survive, grow and reproduce (e.g. Ameztegui and Coll 2011; Ligot et al. 2013). The exact needs in
84 terms of variablity in light availability ultimately depend on the interspecific range of shade
85 tolerances (Kobe et al. 1995), but the greater the variability in understory light conditions, the
86 greater the opportunities for multiple species to regenerate. However, the variability in understory
87 light is likely positively correlated with the average quantity of light transmitted through the canopy.
88 As canopy openness increases, both the mean and the range of understory light conditions increase
89 (Canham et al. 1990). Since canopy transmittance is hypothesized to decrease with forest
90 heterogeneity, variability in understory light should also decrease with forest heterogeneity.
91 Sustainable management of heterogeneous forests should therefore optimize both the capture of

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solar radiation by overstory trees and by understory seedlings, i.e. it should both minimize mean light transmittance and maximize the variability of light transmittance.

The main question we address in this paper is how does the structural and compositional heterogeneity of the forest overstory affect light interception and the amount and variability of understory light. In particular, our specific questions are: (i) How does overstory structural and compositional heterogeneity affect the total interception of light? (ii) How does structural and compositional heterogeneity of the overstory affect spatial variability of understory light? We hypothesize that stands composed of trees of multiple species and multiple sizes will intercept more light than uniform stands because canopies would be denser with reduced gap area between crowns. Since we expect the variability of light transmittance to be positively correlated with mean light transmittance, we additionally hypothesize that variability in understory light will be reduced with forest heterogeneity.

Methods

Study species

We selected four species for which allometric relationships required to compute canopy light transmittance with three-dimensional radiative transfer models (Ligot et al. 2014b) have been previously calibrated : sessile oak (*Quercus petraea* (Matt.) Liebl.), European beech (*Fagus sylvatica* L.), mountain pine (*Pinus uncinata* Ram ex. DC) and silver fir (*Abies alba* Mill.). In the first study from which species calibrations were determined, Ligot et al. (2014a) monitored 27 mixed stands of sessile oak and European beech in the Belgian Ardennes (50°15'N, 5°40'E). In a second study, Ameztegui and Coll (2011) monitored 24 mixtures of mountain pine and silver fir in the Spanish Pyrenees (42°20'N, 1°40E). These study species provided us with a large gradient of species shade tolerance

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and adult tree crown properties. In particular, the four study species spanned a gradient from shade tolerant species with very dense and deep ellipsoidal crowns (European beech) to shade intolerant species with sparse and small parabolic crowns (mountain pine). By increasing order of shade tolerance, the list of the study species is pine, oak, fir and beech (Niinemets 2006).

Creating virtual stands

To examine how overstory heterogeneity influences the mean and the variability in understory light conditions, we simulated 90 contrasted forest stands including 3 typical forest structures (single-layered, multi-layered with two or three vegetation layers and reverse J-shaped distribution), 10 mixtures of forest composition based on combinations of the four species (beech, oak, beech/oak, pine, fir, fir/pine, oak/pine, beech/fir, beech/oak/pine, beech/fir/pine), and 3 levels of basal area (15, 25 and 35 m^2ha^{-1}) (Fig. 1). Each virtual stand was 50 x 50 m, and since the position of the trees was randomly drawn from a uniform distribution, each combination was simulated 100 times. We chose a uniform distribution because we found no general evidence of aggregated or regular distributions of trees in stands of the studied species (the values of the aggregation index Clark-Evans were generally close to 1, see Table 1). The resulting tree spatial distribution of most simulated plots was random (Clark-Evans' index close to 1, range 0.74 to 1.41).

Tree diameters at breast height (DBHs) in the virtual stands were drawn from statistical distributions, depending on the stand structure. To create single-layered stands, tree DBHs were drawn from a truncated normal distribution with two parameters, $N(\mu_1= 30$ cm, $\sigma_1= 4.5$ cm, min=6 cm, max=70 cm$)$, and with all species occupying the same canopy layer. In multi-layered stands composed of two species, tree DBHs were drawn from two truncated normal distributions: $N(\mu_1=$ 40 cm, $\sigma_1 = 6$ cm, min=6 cm, max=70 cm$)$, and $N(\mu_2 = 25$ cm , $\sigma_2 = 3.75$ cm, min=6 cm, max=70 cm$)$. In multi-layered stands composed of three species, tree DBHs were drawn from the two previous distributions and from a third one: $N(\mu_1 =$ 35 cm, $\sigma_1 = 3.75$ cm, min=6 cm, max=70 cm$)$. The standard

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deviation of DBHs was set to correspond to a coefficient of variation of 15%. In mixed multi-layered stands, the less shade-tolerant species occupied the upper vegetation strata. To create a reverse j-shape structure, tree DBHs of all species were sampled from a single truncated exponential distribution: *exp(k)* with *E(DBH) = 1/k = 25 cm, min=6 cm, max=70 cm*. Altogether these distribution parameters ensured that the quadratic mean diameter of all simulated stands was relatively similar (about 30 cm). In mixed stands composed of two or three species, each species was assigned 50% or 33% of the total basal area, respectively.

This experimental design crossing levels of canopy density, composition and structure would not have been possible with field experiments. It would be illusory to search for representative stands of every combination of these three factors without interference with other factors (e.g. canopy gaps, stand edges, site conditions).

The choice of the simulated levels of basal area, shapes and parameters of DBH distributions and species mixtures was critical as a different choice would have led to different results. Even though most of the simulated stands spanned a realistic range of conditions (Table 1), some of them are rather theoretical (e.g. mixtures of 3 species). However, the light model we used (see next section) is assumed to synthesize our knowledge of radiative transfer through forest canopies and to be valid for different forest structures and compositions.

Tree height and crown radius were computed using species-specific allometric relationships determined by Ameztegui and Coll (2011) and Ligot et al. (2014a) (Fig. 2). Leaf area density (LAD) was set according to previous measurements (Ligot et al. 2014a) to 0.71 m^2m^{-3} for beech and 0.52 m^2m^{-3} for oak. For both pine and fir, LAD was set to 0.6 m^2m^{-3} based on the literature (Ligot et al. 2014b). Moreover, small variations in LAD around 0.6 have been shown to have little effect on light interception simulations (Courbaud et al. 2003; Ligot et al. 2014a).

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Modeling understory light

The amount of light available in the forest understory of each simulated stand was computed with SAMSARALIGHT (Courbaud et al. 2003; Ligot et al. 2014a), a three-dimensional radiative transfer model[1] implemented in a library of the CAPSIS platform (Dufour-Kowalski et al. 2012). This model has proven to satisfactorily predict understory light in uneven-aged forests of Norway spruce in the Alps (*Picea abies* (L.) Karst) (Courbaud et al. 2003), in Belgian mixtures of oak and beech forests (Ligot et al. 2014a) and in Spanish mixtures of fir and pine in the Pyrenees (Appendix A1).

For this experiment, SAMSARALIGHT was set to compute light interception using Beer's law (Eq. 1). Beer's law describes the attenuation of a monochromatic ray within a turbid medium, i.e. a medium made up of small elements randomly scattered and presenting a homogeneous transparency (Brunner 1998). Briefly, the probability of beam interception ($1-\tau$) by canopy elements is a function of the canopy element density (leaf area density, *LAD*, in $m^2\ m^{-3}$), the path length of a ray through the canopy (l, in m), the extinction coefficient (k) and the clumping factor (Ω). K and Ω depend on canopy element inclination and spatial distribution:

$$\tau(\eta,\gamma)=exp(-k\cdot\Omega\cdot LAD\cdot l(\eta,\gamma)) \qquad \text{Eq. 1}$$

Tree crowns of hardwood and softwood species were modeled with three-dimensional ellipsoidal and parabolic shapes, respectively, using the allometric relationships from Ligot et al. (2014a) and Ameztegui and Coll (2011). In SAMSARALIGHT, individual tree crowns were considered as homogeneous turbid media. For each month of the growing season (from April to October), 130 diffuse and 81 direct light ray directions were sampled. Diffuse ray directions were sampled over the sky hemisphere at regular zenith angles above a starting value of 10°. Similarly, direct ray directions were sampled every hour over the average monthly solar trajectory. For every direction, parallel rays

[1] A version of this software can freely be downloaded at http://orbi.ulg.ac.be/handle/2268/187361 (accessed on the 15th April 2016).

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were cast at the centers of each 25 m^2 ground cell. To remove edge effects, SAMSARALIGHT uses an algorithm that considers plots as being wrapped around a torus (Courbaud et al. 2003). The radiation transmitted to a cell by a light beam depended on the radiation absorption of the succession of crowns that are crossed. The amount of radiation available over a vegetation season for each cell was obtained by cumulating the radiation from light coming from every direction. The amount and angular distribution of incident diffuse and direct lights were computed assuming all sites had latitude of 50°N (i.e. the latitude of the Belgian sites). Simulating light interception at the lower latitude of the Spanish sites (42°N), did not alter our conclusions (results not shown). While latitude affects absolute values of irradiance, the transmittance (i.e. the ratio between the irradiances available above and below forest canopy) is not much affected by latitude.

Statistical analyses

In order to determine the relative importance of the three studied factors (stand composition, structure and basal area), two three-way ANCOVAs were carried out. The response variables were the mean and the standard deviation of light transmittance, i.e. the proportion of incident light transmitted to the understory, computed for each simulation run and each cell. The standard deviation of light transmittance was used as an indicator of the variability of light conditions in the understory. Stand composition, structure and basal area were considered as fixed factors with nine, two and one degrees of freedom, respectively. Since some interactions among factors were significant, multiple one-way ANCOVAs were carried out to further analyze the effect of each factor. To test the differences between the means of factor levels, we used Tukey's "Honest Significant Difference" method (R Core Team 2013). We graphically examined model residuals to verify that ANCOVA assumptions were fulfilled (i.e. normal distribution of residuals, equal variance among groups, homoscedasticity, and linear relationship). All statistical analyses were performed with R software (R Core Team 2013).

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Results

Mean transmittance

Mean light transmittance (m_T) depended on forest composition (62.5% of the total explained variance) and basal area (33.0%), as indicated by type II sum of squares, whereas the interactions between composition and basal area (2.9%), forest structure (1.4%) and the other interactions among factors (0.2%) had minor effects (Table 1). A gradient of mean transmittance was observed in relation to stand composition. Light transmittance was the lowest (i.e. tree light interception was the greatest) in the most shade-tolerant pure beech stands (m_T = 4.8 % on average, ± 4.3 % of standard deviation) while transmittance in the least shade-tolerant pure pine stands was the greatest (43.0 ± 11.5 %). As expected, mean transmittance clearly decreased with basal area. For instance, the mean transmittance in oak stands with basal area of 15 and 35 m^2 ha^{-1} were 28.7 % (± 2.36 %) and 7.6 % (± 1.31 %), respectively.

Mean transmittance of mixed stands was always intermediate between the transmittance in corresponding pure stands (Fig. 3) and always lower than the weighted average of transmittance in corresponding pure stands (weighted by species basal area proportion). For example, transmittance in mixtures of oak/pine (25.9 ± 10.8 %) was intermediate between pure stands of oak (lower light transmitted, 16.9 ± 9.0 %) and pine (higher light transmitted, 43.0 ± 11.5 %) and lower than the weighted average (29.9%). In the case of mixtures of three species, transmittance was intermediate between the transmittance of the corresponding two most shade-tolerant species mixtures and the transmittance of the pure stand of the most shade-intolerant species although the amount of transmitted light was usually closer to that found in mixtures of the two shade-tolerant species. Again as an example, in beech/fir/pine mixtures, light transmittance (14.1 ± 8.3 %) was slightly greater than in beech/fir mixtures (the two more shade-tolerant species in the mix, 9.2 ± 6.5 %). The

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transmittance values in mixtures of 2 or 3 species were in average 3.6 and 9.2% lower than the weighted average, respectively.

Although forest structure had a statistically significant effect on the mean of transmittance, its effect was weaker than that of stand composition or basal area (Table 1). In pure stands, transmittance increased with the number of tree layers, being the lowest in single-layered stands (18.1 ± 13.9 %) and the highest in reverse j-shaped stands (21.0 ± 14.8 %). In mixed stands, the mean transmittance of multi-layered stands was in some cases significantly greater than in even-sized stands but in all cases remained lower than in reverse j-shaped stands (Fig. 3).

Transmittance variability

Similar to mean transmittance, the variability in transmittance depended mostly on forest composition (71.5% of total explained variance, Table 2) and basal area (23.9%). Forest structure (1.2%) and interactions among factors (3.4%) had little effect. The variability in transmittance was also lowest in beech stands and increased according to species shade tolerance (beech < fir < oak < pine), with the exception of pine stands, for which the variability in transmittance was lower than in fir stands. The differences between the variability in transmittance of pine and fir stands were significant for basal area values of 15 and 25 m^2 ha^{-1}. As expected, mean transmittance and standard deviation were positively correlated ($r = 0.759$, $p < 2.2E\text{-}16$). Nevertheless, the relationships between these two variables departed from a linear relationship with a maximum variability in transmittance observed at about a mean transmittance of 40%.

For some combinations of stand structure, composition and basal area, the variability in transmittance in two-species mixtures was greater than the variability in corresponding pure stands (Fig. 4). This happened, for example, in oak and beech mixtures at low basal areas, as well as in the pine and fir mixtures in high-density stands. These relationships were consistent across the three

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253 modelled stand structures. No additive effect was, however, observed when softwood species were
254 mixed with hardwood species.

255 Similar to the results of mean transmittance, the variability in transmittance (σ_T) slightly
256 increased with the number of tree layers in pure stands, being the lowest in single-layered stands (σ_T
257 = 7.5 % on average, ± 3.9 % of standard deviation) and the highest in stands with a reverse j-shaped
258 structure (8.2 ± 3.8 %). In mixed stands, the variability in transmittance of multi-layered stands was in
259 some cases significantly greater than in even-aged stands but remained in all cases lower than in
260 reverse j-shaped structure stands.

261 The variability in transmittance generally decreased with stand basal area (Fig. 4). Nevertheless,
262 there was a significant interaction between basal area and stand composition (Table 2). The effect of
263 basal area on variability in transmittance was lower in pure stands of shade intolerant or mid-
264 tolerant species (e.g. pine and oak) than in stands of shade-tolerant species (e.g. beech and fir).

265 *Discussion*

266 *Tree light capture and overstory heterogeneity*

267 In contrast to our first hypothesis, we found no evidence that increasing structural heterogeneity
268 reduces forest canopy light transmittance or increases tree light interception. Light transmittance
269 even slightly increased with increasing forest structural heterogeneity. Stands composed of one
270 homogeneous tree layer transmitted less light than stands with two or more tree layers. These
271 results are in the line with the higher productivity of pure stands with low size heterogeneity
272 (Bourdier et al. 2016).

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On the other hand, the light transmittance in mixed stands was always lower than the weighted average of transmittance in the corresponding pure stands. Such a results supports the hypothesis that complementarity of light use could be at the origin of the over-yielding that has been observed in some mixed stands (Pretzsch and Schütze 2009; Toïgo et al. 2015; Vallet and Pérot 2011). The difference between the observed values of transmittance in mixed stands and weighted averages originates from the non-linearity of the relationship between light transmittance and stand basal area (Comeau and Heineman 2003; Lochhead and Comeau 2012; Sonohat et al. 2004).

However, other factors likely affect forest productivity as our results are insufficient to explain the absence of over-yielding reported for mixtures such as oak-pine and oak–beech mixtures (Toïgo et al. 2015). In addition to the interception of light, light use efficiency (Onoda et al. 2014) and belowground resources also influence forest growth conditions (Richards et al. 2010) and the understory (Granhus et al. 2016). Despite subordinates trees receive less light than taller trees. Subordinate trees tend to use intercepted light more efficiently producing greater amount of biomass per unit of light interception than taller trees (Onoda et al. 2014). In addition, Toïgo et al. (2015) found over-yielding growth in tree mixtures to increase when soil fertility is low (Toïgo et al. 2015). In a recent review, Forrester (2014) showed that net complementary effects in mixed-forests depend on the spatial and temporal variability in both above- and belowground resources. They stressed the need for further studies to quantify both the conditions (e.g. environmental gradients) and the processes driving these patterns (i.e., over-yielding, complementary effects)

A potential limit of our approach is that the optimization of light capture in our simulated forest stands is restricted by limited crown plasticity, constrained by allometries and a random spatial distribution of trees. Allometries only roughly estimate individual crown development as they assume that the lateral growth of a tree crown is isotropic and independent of the past and present surrounding canopy. Yet, anisotropic crown growth and crown plasticity have been mentioned to be

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297 important in canopy closure (Purves et al. 2007; Vepakomma et al. 2008; Vepakomma et al. 2011).
298 Additionally since in many regions tree growth and survival depend on light transmittance the
299 natural spatial distribution of trees might deviate from a random distribution in order to optimize
300 light capture. Forest management also alters the spatial distribution of trees but often tends to
301 regularize it. Because of our approach to modeling crown dimensions and the spatial distribution of
302 trees, we may thus underestimate the complementarity of light use in heterogeneous forests.
303 Nevertheless, a closed layer of foliage encountered in dense monospecific even-sized stands is
304 sufficient to capture most of the available light, as shown by the lack of ground vegetation and
305 seedlings in dense even-sized stands (e.g. Bailey and Tappeiner 1998).

306 Our findings also underline the importance of forest composition and density on light
307 transmittance. In contrast to the literature (e.g. Lochhead and Comeau 2012; Messier et al. 1998),
308 stand composition had the strongest influence on understory light in our simulations. Stand density,
309 as measured by basal area, was the second most important factor while the heterogeneity in tree
310 size affected little (approx. 1 %) understory light levels in comparison to the two other factors. The
311 order of importance of the tested factors may however depend on the chosen study species and
312 levels of basal area. We studied species with contrasted crown shapes and sizes. The effect of the
313 overstory composition on understory light availability is usually explained by differences in species
314 morphological traits related to light interception (Coll et al. 2011). In our case, leaf area density was
315 relatively similar among the studied species (range between 0.5 and 0.7 m^2 m^{-3}) but crown
316 allometries differed greatly (Fig. 2) and these relationships have been shown to critically affect
317 canopy packing (e.g. Beaudet et al. 2002; Ligot et al. 2014a). In our study, the largest differences in
318 average transmittance were observed between the simulated softwood and hardwood stands, with
319 softwood species (pine and fir) having narrower and smaller crowns than hardwood species (oak and
320 beech), thus transmitting more light (Valladares 2003). However, this result is not generalizable as

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the studied hardwood and softwood species were species of different shade tolerances (Valladares and Niinemets 2008) with the hardwood species being the most shade-tolerant species. In addition, Individuals of the two studied softwood species grow at higher elevations and in colder sites than those of the two studied hardwood species, with consequences both on allometries and on leaf area density (Astrup and Larson 2006; Lefrançois et al. 2008; Leuschner et al. 2006; López-Serrano et al. 2005).

Variability of understory light and overstory heterogeneity

In contrast to our second hypothesis, we did not find a systematic decrease in the range of understory light conditions with overstory heterogeneity. Instead, increasing tree size heterogeneity and especially species heterogeneity resulted in significantly greater variability of understory light conditions, depending on stand composition and basal area. For example, beech, a very shade tolerant species, maintained a very dark understory (low mean and variability of transmittance) even at moderate basal area (e.g. 25 m^2 ha^{-1}). Adding beech in mixtures with oak generally limited the variability of understory light except in stands with very low basal area (15 m^2 ha^{-1}). In contrast, the variability of understory light in mixtures of pine and fir was greater than in the corresponding pure stands of either pine or fir, when basal area was high (≥ 25 m^2 ha^{-1}). Forest structure, i.e. the organization of trees in different vertical strata, little affected the variability in understory light conditions. In pure stands, the variability in transmittance increased with the number of tree strata, but in mixed stands, the lack of difference between single-layered and multi-layered stands was not expected. Although an earlier study in mixed hardwood stands in North-East America found little variation in light transmittance with stand age and thus canopy strata complexification (Brown and Parker 1994). However, we acknowledge that this result may be influenced, at least in part, by the approach we used to generate mixed stands: Mixed, single-layered stands were composed of two species in one single tree layer, with trees of about the same DBH but varying height depending on

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specific allometries. Therefore, the comparable understory light variability observed between single-layered and multi-layered stands may be due to a lack of sufficient differences in the heterogeneity of tree sizes for these two structures.

The variability in understory light and the mean transmittance through the canopy are positively correlated and hence influenced by similar factors. Both the mean and the variability of transmittance increases as the size of canopy gap increases (Canham et al. 1990; Hardy et al. 2004). Nevertheless, our results further suggest that the relationship is not linear. As corroborated by the data of Da Silva et al. (2011), the variability in understory light is presumably maximized for a certain level of canopy openness that corresponds in our study to an approximate mean transmittance of 40 %. At low understory light conditions (m_T < 40 %), the frequency distribution of transmittance is typically right-skewed as most understory patches are in low light conditions and few are in high light conditions (Beaudet et al. 2011). The variability in transmittance then increases with mean transmittance, e.g. increased overstory heterogeneity or decreased overstory density. In contrast, in high light conditions (m_T > 40 %) a reduction in mean transmittance could lead to an increase in transmittance variability, e.g. when a shade-tolerant species was mixed in a stand with less shade-tolerant species.

Research perspectives

Our findings were obtained through the simulation of stands with a random spatial distribution of trees, fixed levels of basal area and constant quadratic mean diameters of 30 cm. Even though the studied stands were constructed with relatively arbitrary parameters (DBH distribution, composition, basal area), the characteristics of most simulated stands spanned typical conditions found in managed forests of the study species (Table 1) and for these stands the predictions of understory transmittance are well in the range of observed values (Fig. A2). However, further work remains to be done before generalizing our results especially in stands with varying diameters or particular

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369 spatial distributions of trees (Ngo Bieng et al. 2006), e.g. aggregation of tree species or aggregation of
370 understory trees in overstory gaps. The former is presumably a key variable of stand structure on
371 understory light (Bourdier et al. 2016) as understory light should increase with stand quadratic mean
372 diameter for a given level of basal area (Ligot et al. 2014a; Lochhead and Comeau 2012).

373 In addition, further modeling efforts are required to analyze the impact of even-aged and
374 uneven-aged silviculture on understory light conditions. Uneven-aged silviculture maintains relatively
375 constant basal area (e.g. about 30 m^2 ha^{-1} in spruce stands with periodic removals of 5-10 m^2/ha)
376 while in even-aged silviculture basal area varies greatly (e.g. from 0 to 60 m^2 ha^{-1}) during a rotation
377 (i.e. the full cycle from small regeneration to mature stand). A comparison of the effect of these two
378 silviculture regimes on resource acquisition and use by forest stands therefore requires analyses that
379 consider the change of forest structure during a complete rotation.

380 An investigation of the influence of individual plasticity of crown geometry such as light induced
381 plagiotropy and leaf area density should also be performed as these traits are known to be affected
382 by openings and stand composition (Mitchell 1975; Piboule 2001; Purves et al. 2007; Strigul et al.
383 2008; Umeki 1996, 1997). As we repeated our simulation 100 times, this effect has probably been
384 partly minimized. Nonetheless, the extent to which individual crowns can expand in reaction to the
385 local environment and how this affect understory light needs to be further studied.

386 # *Conclusion*

387 The advantage of heterogeneous forest stands may lie in opportunities to naturally regenerate
388 various species in the understory as well as in opportunities to enhance light capture by the
389 overstory. This study has taken a step in the direction of better understanding the effects of forest
390 heterogeneity on light capture and light distribution between the canopy and regeneration layers,

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which is a necessary step in the current debate on increasing forest heterogeneity as a technique for making forest management more sustainable.

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Tables

Table 1: A brief description of the plots monitored in oak-beech mixtures by (Ligot et al. 2014a) and in fir-pine mixtures by (Ameztegui and Coll 2011). The table indicates the number of studied plots (n), the average (minimum and maximum) measured quadratic mean diameter (Dg), coefficient of variation of tree diameters (CV), stand basal area, Clark-Evans aggregation index and transmittance. Regular distributions of trees have Clark-Evans values greater than 1 while aggregated distributions have a Clark-Evans value lower than 1 (Clark and Evans 1954).

Species	n	Dg	CV	Basal area	Clark-Evans	Transmittance
		Cm	%	m^2/ha	-	%
Oak-Beech[1]	27	42.4 (30.0-54.9)	43 (27-60)	18.0 (7.5-35.0)	1.1 (1.0-1.3)	22.8 (0.8-62.6)
Oak-Beech[2]	2773	36.0 (6.9-87.3)	38 (0.0-150.5)	20.0 (1.2-70.4)	-	-
Fir-Pine[3]	24	30.6 (19.53-42.0)	36 (15-53)	23.3 (7.6-44.5)	0.9 (0.5-1.2)	

These figures came from ([1]) Ligot et al. (2013),([2]) the permanent inventory of forest resources in Wallonie (Lecomte 2013) and ([3]) Ameztegui and Coll (2011)

Table 2: ANCOVA table of the mean transmittance (aggregated by simulation run). The table indicates, for each factor and interactions, the degrees of freedom (Df.), the type II sum of squares (SumSq.), the percentage of total sum of squares (Sum Sq. %), the mean square (Mean Sq.), F and P values. The R^2 of this model is 97%.

	Df.	Sum Sq.	Sum Sq. %	Mean Sq.	F value	P value
basal area	1	596270	32.99	596270	114564	0.00E+00
Composition	9	1129719	62.50	125524	24118	0.00E+00
Structure	2	24854	1.37	12427	2388	0.00E+00
basal area * composition	9	52436	2.90	5826	1119	0.00E+00
basal area * structure	2	891	0.05	445	86	1.51E-37
composition * structure	18	2896	0.16	161	31	3.58E-103
basal area * composition * structure	18	550	0.03	31	6	2.54E-14
Residuals	8940	46530		5		

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589 Table 3: ANCOVA table of the standard deviation of transmittance predictions: degree of
590 freedom (Df.), the type II sum of squares (Sum Sq.), the percentage of total sum of squares, mean
591 squares (Mean Sq.), F value and P value. The R^2 of this model is 88%

	Df.	Sum Sq.	Sum Sq. %	Mean Sq.	F value	P value
basal area	1	28748	23.91	28748	16042	0.00E+00
Composition	9	85970	71.51	9552	5330	0.00E+00
Structure	2	1453	1.21	726	405	3.20E-169
basal area * composition	9	3530	2.94	392	219	0.00E+00
basal area * structure	2	78	0.07	39	22	3.40E-10
composition * structure	18	312	0.26	17	10	2.86E-27
basal area * composition * structure	18	133	0.11	7	4	8.52E-09
Residuals	8940	16021		2		

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Figure captions

Fig. 1: Examples of three virtual stands with basal area of 25 m²/ha: a single-layered stand of European beech with a mean DBH of 35 cm (a); a multi-layered stand of sessile oak and beech with mean DBHs of 15 cm for beech (green) and 35 cm for oak (purple) (b); and a reverse J-shaped stand of mountain pine (blue) and silver fir (gray) with mean DBHs of 25 cm (c). Understory light was assessed for each cell. Levels of transmittance under the trees are represented by a gradient of color from black (transmittance of 0-10%) to yellow (90-100%).

Fig. 2: Allometric relationships of the four study species, based on Ligot et al. (2014a) and Ameztegui and Coll (2011).

Fig 3: Average light transmittance for 90 virtual forest stands as a function of forest composition, forest structure and basal area. The letters above the boxplots indicate significantly different groups ($\alpha = 0.05$).

Fig 4: Light variability in the forest understory of 90 virtual forest stands as a function of forest composition, forest structure and basal area. The letters above the boxplots indicates significantly different groups ($\alpha = 0.05$).

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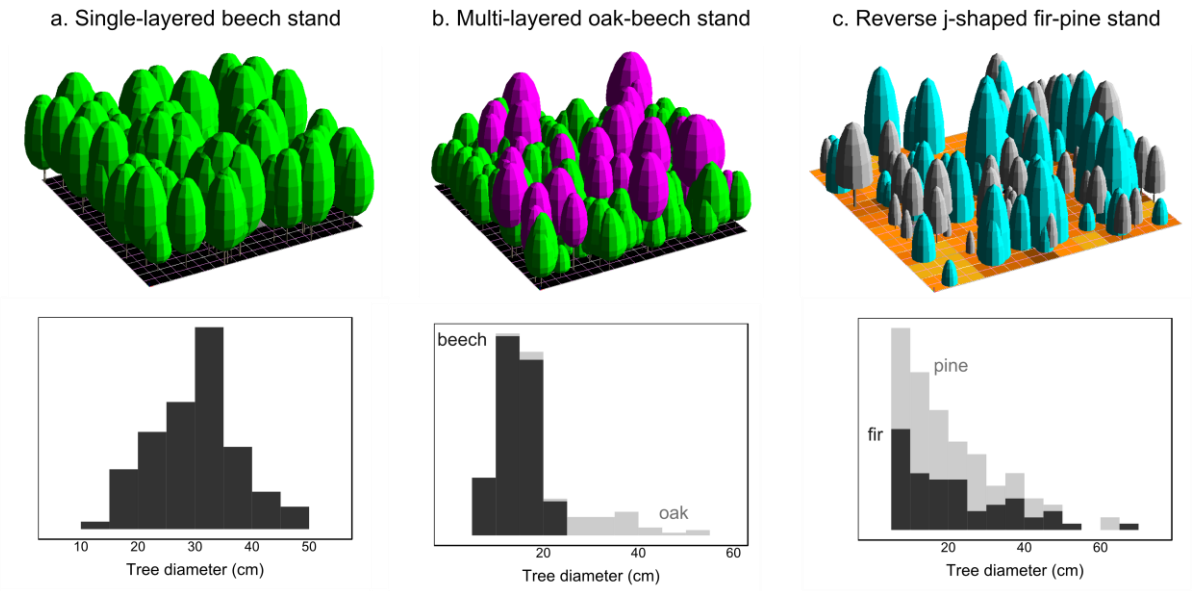
609 # *Figures*

610 Fig. 1



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613 Fig. 2

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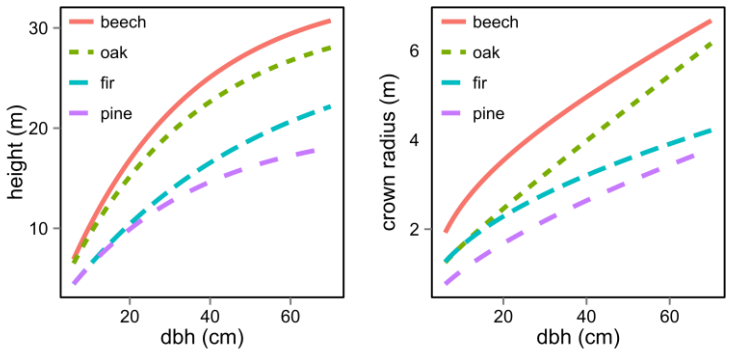

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616 Fig. 3

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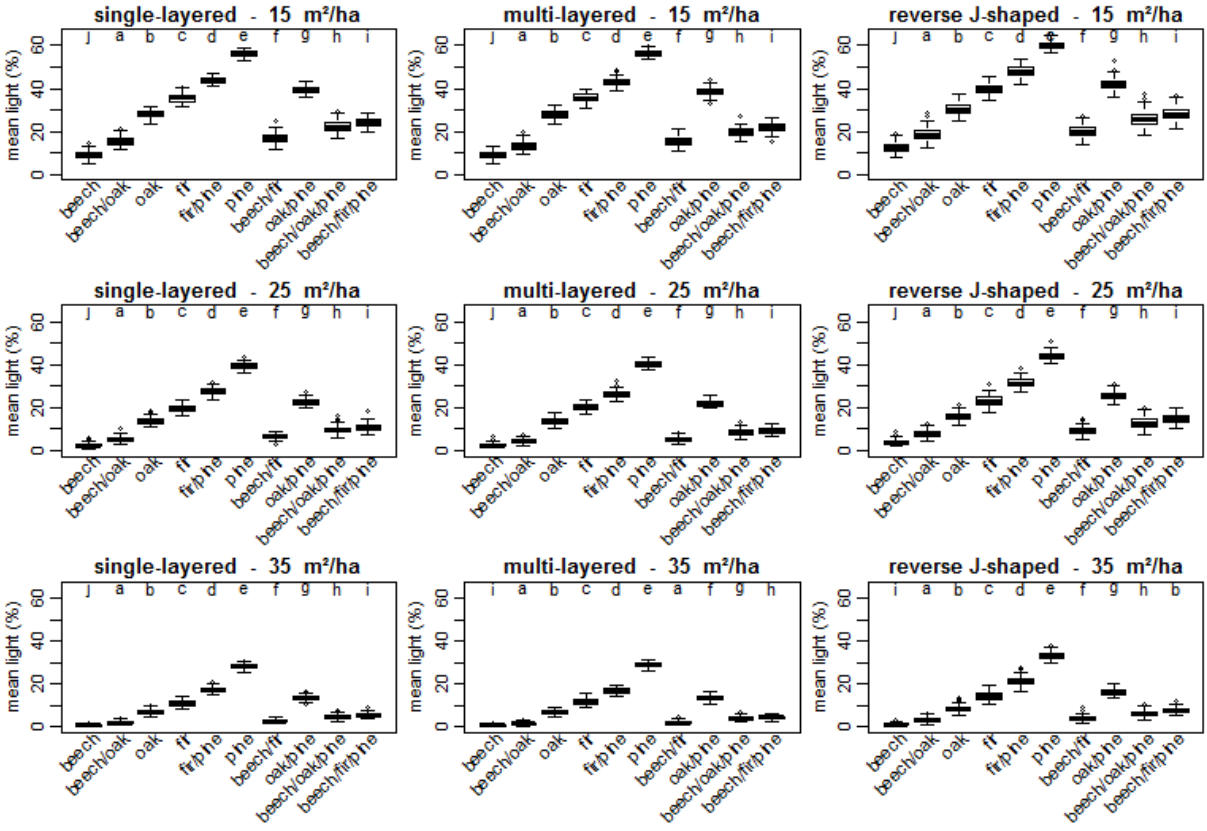

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620 Fig. 4

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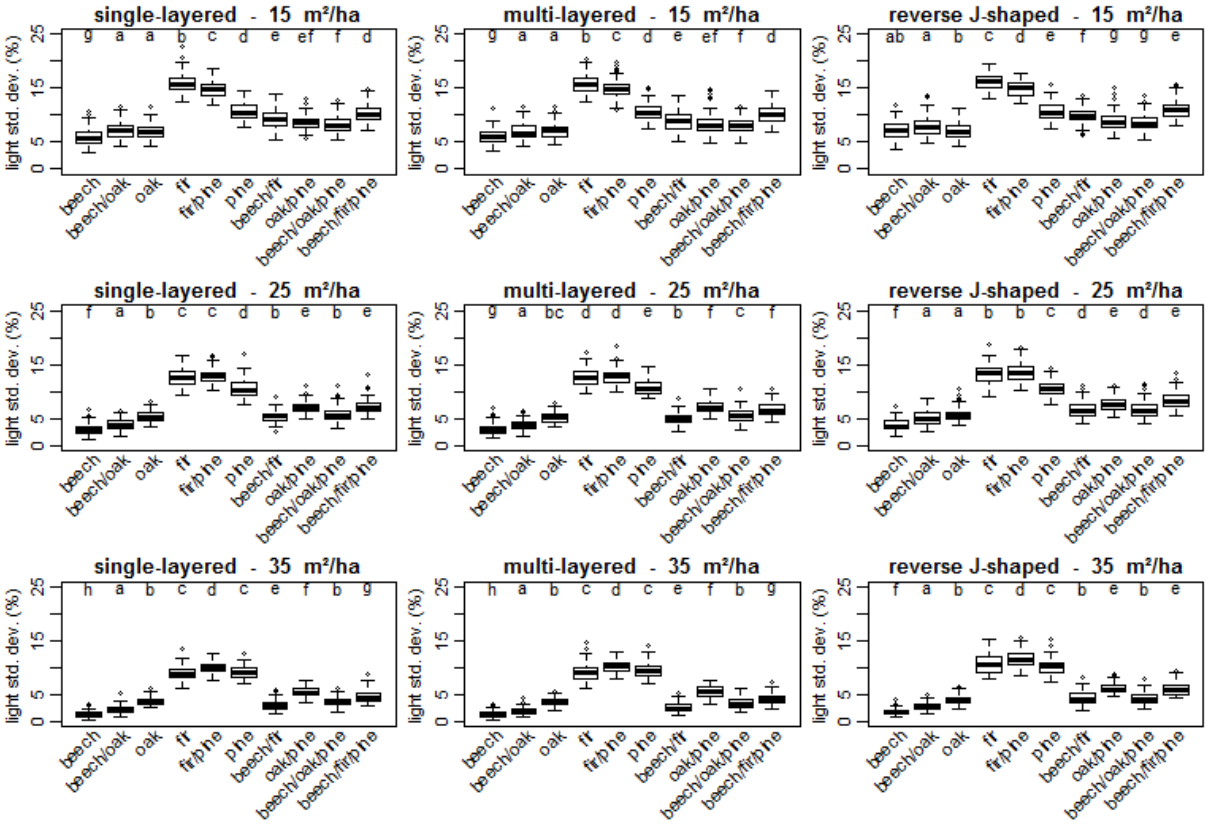

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Appendices

Appendix A1: Validation of samsaralight

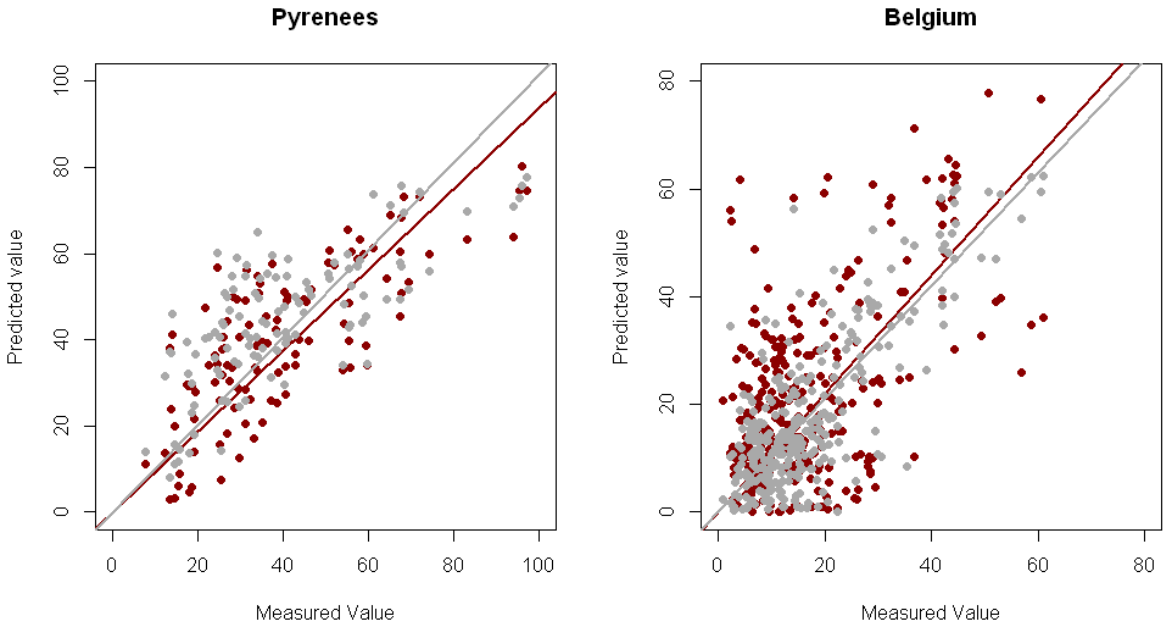

Fig.A1: Comparison of prediction and measures with hemispherical photographs of transmittance in Spanish forests composed of mountain pine and silver fir (on the left) and Belgian forests of European beech and oak (on the right). Predictions were computed with two radiative transfer models: SORTIE-ND (in red) and SAMSARALIGHT (in grey). SAMSARALIGHT model was chosen to perform the simulation of this study and its performance was further described by Ligot et al. (2014a).

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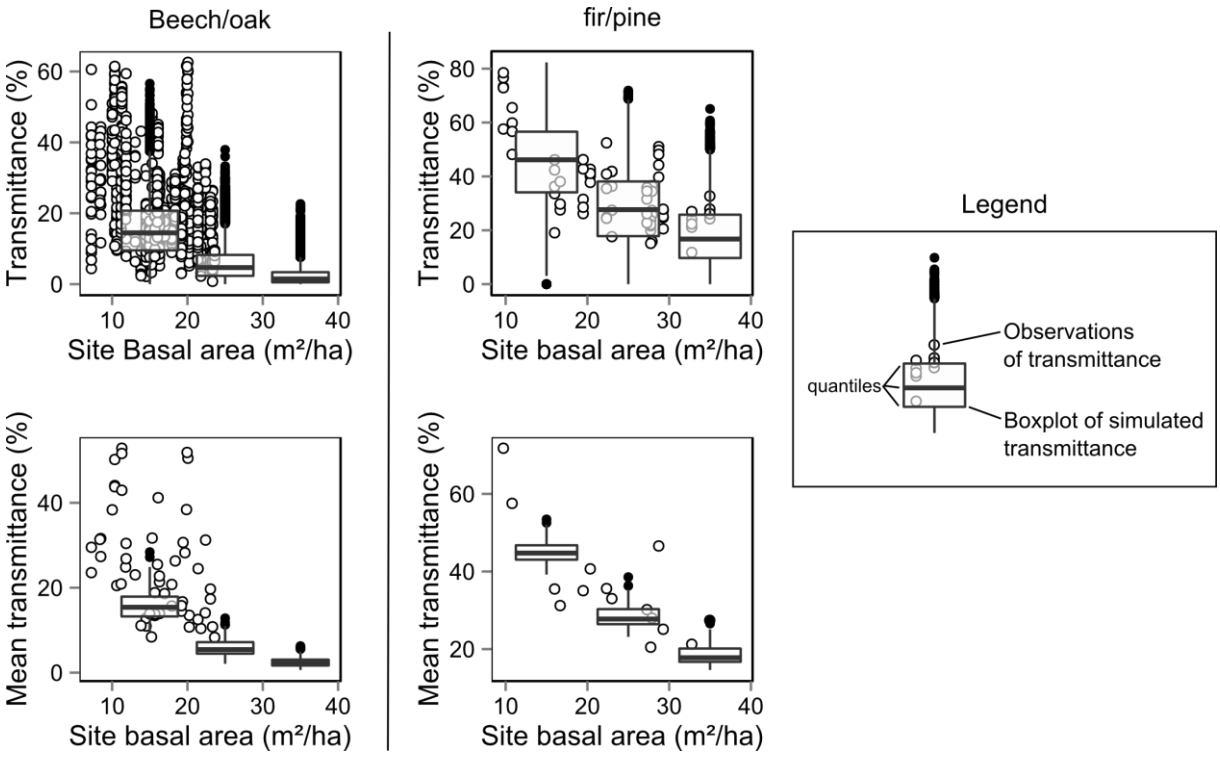

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634 Fig A2: Comparison of the simulated values of transmittance and values of transmittance recorded in
635 previous studies along a gradient of stand basal area. The two plots on the left show values for
636 mixtures of oak and beech (Ligot et al. 2013) while the two plots on the right show values for fir and
637 pine mixtures (Ameztegui and Coll 2011). Simulated values are depicted with boxplots while
638 observed values are depicted with empty dots. Ligot et al. (2013) did not sample plots along the
639 whole basal area gradient – even though such stands exist (Table 1) - because their study focused on
640 partially open forests with natural regeneration.

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