

Replace me if you can: Abundance of advance regeneration under canopy trees in a primeval beech forest

R. Petrovska^{a,b,*}, H. Bugmann^b, M.L. Hobi^a, P. Brang^{a,1}

^a Swiss Federal Institute for Forest, Snow and Landscape Research, WSL/Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

^b Forest Ecology, Department of Environmental Systems Science, ETH/Universitätstrasse 16, 8092 Zurich, Switzerland

ARTICLE INFO

Keywords:

Acer platanoides
Acer pseudoplatanus
 Background mortality
 Dominance
Fagus sylvatica
 Abundance
 Replacement
Ulmus glabra

ABSTRACT

Tree replacement patterns strongly shape species coexistence and dominance in forest ecosystems. In mixed forests subject to a small-scale disturbance regime, dead canopy trees are often replaced by advance regeneration. We studied the abundance of saplings (6–10 cm dbh) and poles (10–25 cm dbh) under canopy trees based on four inventories on a 10-ha permanent plot in a large primary forest dominated by *Fagus sylvatica* in Ukraine. Saplings and poles of *Fagus sylvatica*, *Acer platanoides*, *A. pseudoplatanus* and *Ulmus glabra* were spatially linked to canopy trees ('hosts', dbh > 25 cm) based on their crown radius, and the hosts' neighborhood was classified according to the presence of dead trees. The number of saplings and poles under hosts was modelled with a Bayesian approach. There was a higher number of advance regeneration under hosts with increasing host diameter. The abundance of advance regeneration was the lowest under hosts in the canopy (i.e., under shaded conditions) and highest for hosts growing in gaps. 1) Under the canopy, only *F. sylvatica* poles can replace heterospecific hosts > 80 cm dbh, while other pole species are clearly below the replacement threshold. 2) Near dead lying trees, *Acer pseudoplatanus* rarely achieved an abundance of one pole at a host dbh > 80 cm. 3) In gaps, *Acer* spp. poles were able to replace *F. sylvatica* hosts. The proximity to dead lying trees and gaps is crucial for *Acer* spp. and *U. glabra* saplings for recruitment to the pole stage. The higher rate of recruitment under hosts adjacent to dead lying trees suggests that the total length of gap edges may be as important as gap size or disturbance frequency. In gaps > 550 m², advance regeneration without hosts (growing in gaps) of *Acer* spp. can recruit higher number of saplings than *F. sylvatica*, but not poles. We conclude that almost all canopy trees of *Acer* spp. and *U. glabra* are likely to be replaced by *Fagus sylvatica* if the current small-scale disturbance regime and single-tree mortality continue to prevail.

1. Introduction

An important process in forest succession is the replacement of a dead canopy tree by the tallest or fastest growing individual beneath it (Fox 1977), which may lead to a change in tree species composition. Canopy tree replacement has often been investigated in old-growth forests (Brewer and Merritt 1978; Poulson and Platt 1996; Woods 1979, 1984) as its patterns may provide insight into mechanisms of species coexistence or dominance (Busing 1996) and the nature of community dynamics (Horn 1975). In primary beech-dominated (*Fagus sylvatica* L., European beech) forests that are characterized by a small-scale disturbance regime (Hobi et al. 2015) and a canopy turnover time between 100 and 220 years (Drößler and Von Lüpke 2005; Valverde

and Silvertown 1997), canopy tree replacement by poles (10–25 cm dbh, diameter at breast height) occurs mostly due to two processes, as explained below.

First, background mortality of individual trees (>25 cm dbh, Nagel et al. 2010), i.e. mortality that occurs in the absence of distinct disturbance events creates small gaps (<100 m²), representing an important process that is structuring old-growth forests (Franklin et al. 1987; Korpel', 1995; Taccoen et al. 2019). Dying trees gradually lose crown biomass and let more light penetrate to the lower layers of the canopy, thus triggering the growth of advance (pre-established) regeneration beneath and facilitating subsequent replacement.

Second, intermediate wind disturbance events create mid-sized openings (100–1,500 m²) that have no discrete edges and may contain

* Corresponding author.

E-mail addresses: roksolana.petrovska@wsl.ch (R. Petrovska), harald.bugmann@usys.ethz.ch (H. Bugmann), martina.hobi@wsl.ch (M.L. Hobi).

¹ Deceased 2022.

surviving trees (Nagel and Diaci 2006; Woods 2000). Such openings stimulate the rapid growth of suppressed saplings (5–10.0 cm dbh) of *Acer platanoides*, *Acer pseudoplatanus* (Norway and sycamore maple), *Fagus sylvatica* and, occasionally, *Ulmus glabra* (wych elm) (Caquet et al. 2010; Feldmann et al. 2020; Janík et al. 2016; Kuchel et al. 2010).

To our knowledge, only two studies have reported reciprocal species replacement (i.e., saplings of two competing species are similarly able to replace dying canopy trees of the other species) between conifers and *Fagus sylvatica* in old-growth forests in Europe (Keren et al. 2014; Nagel et al. 2010), and there is no study on broadleaved species. In contrast, replacement among broadleaved species has often been studied in North America (Horn 1975; Poulson and Platt 1996; Woods 1979, 1984). While at the early sapling stage, *Fagus sylvatica* and *Acer* spp. often dominate in small and middle-sized gaps (Caquet et al. 2010; Feldmann et al. 2020), typically only *Fagus sylvatica* reaches the pole stage in small gaps (Feldmann et al. 2018). Such differences may maintain or reinforce an existing hierarchy, i.e. the dominant species in the shade will also show the highest growth rate after release among the poles in small and mid-sized gaps. This superior performance is often tied to species-specific differences in shade tolerance (Firm et al. 2009; Lertzman 1992; Nagel and Diaci 2006; Webb and Scanga 2001). Given the strong differences in shade tolerance between the tree species in European broad-leaved primary forests (Ellenberg and Leuschner 2010), individual tree replacement may not be reciprocal under the small-scale disturbance regime of these forests.

The number of poles that are being recruited for the eventual replacement of a broadleaved canopy tree in European temperate forests is poorly known. When a canopy tree is characterized by a long lifespan and slow senescence, a shade-tolerant pole will typically replace it because competing shade-intolerant poles tend to lag too far behind in size compared to shade-tolerant poles (Fox 1977). The mortality rate of canopy trees in *Fagus sylvatica* primary forests increases with tree size (Hülsmann et al. 2016). Therefore, the senescence of either individual canopy trees or tree cohorts is likely to favour their replacement by *Fagus sylvatica* rather than *Acer* spp. or *Ulmus glabra*. Consequently, the number of poles of the same or other species under canopy trees is likely an important element of species co-existence or dominance in primary forests. However, a quantitative understanding of (1) the likelihood of finding saplings and pole-stage trees under canopy trees in beech-dominated forests, and (2) the abundance of such sub-canopy elements is lacking. Here, we adopt an individual-tree perspective to evaluate tree-by-tree replacement (i.e., related to ‘background mortality’).

Primary *Fagus sylvatica* forests often show a striking dominance of beech (Korpel, 1995). For instance, in the Uholka-Shyrokyi Luh reserve (Ukraine), this species makes up around 96% of the basal area (Commarmot et al. 2013). Taking into account the low abundance of the other tree species in this forest, our study focuses on the four most abundant species in this forest and aims to answer the following questions: i) What is the number of advance regeneration (saplings and poles) of *Fagus sylvatica*, *Acer platanoides*, *A. pseudoplatanus* and *Ulmus glabra* under mature canopy trees in this primary forest? ii) Which factors are driving the presence and abundance of the advance regeneration in this forest?

2. Materials and methods

2.1. Study area

The Uholka-Shyrokyi Luh reserve (total area: 10,383 ha) in Ukraine is a beech-dominated primary forest, listed as a UNESCO World Heritage site. The Uholka part covers 4,729 ha and ranges between 400 and 1300 m a.s.l. in elevation. Mean annual temperature is about 8 °C at 430 m a.s.l. (−3 °C in January and 18 °C in July) and mean annual precipitation amounts to 1134 mm (Commarmot et al. 2013). The forest is subject to a small-scale disturbance regime, resulting in mainly small canopy gaps (98% are < 200 m²), and only few large stand-replacing events were

detected using high-resolution satellite imagery (Hobi et al. 2015).

A permanent inventory plot of 10 ha (200 m × 500 m) was established in Uholka in 2000 as a collaboration project between the Swiss Federal Institute for Forest, Snow and Landscape Research WSL and the Carpathian Biosphere Reserve, Ukraine. It has since been re-measured in 2005, 2010 and 2015 (Stillhard et al. 2019). It is located in an old-growth stand and is situated at 48.2695°N, 23.6207°E at an altitude of 700–800 m a.s.l. The plot faces mainly southeast with a grade between 20 and 40%. Soils consist mainly of dystric cambisols (Commarmot et al. 2005). The plot is dominated by *Fagus sylvatica* making up around 95% of the basal area (Stillhard et al. 2019), but it also includes tree species such as *Acer platanoides*, *A. pseudoplatanus*, *Ulmus glabra* and *Fraxinus excelsior*. Since plot establishment, two intermediate wind and heavy snowfall events occurred in 2007 and 2009, resulting in several larger canopy gaps (Fig. 1, Stillhard et al. 2019).

The 10 ha plot is divided into 40 subplots of 50 m × 50 m to facilitate inventory work. Within these subplots, all living and dead trees with a minimum diameter at breast height (dbh, height = 1.3 m) of 6 cm were numbered and mapped (Stillhard et al. 2019). Species identity and dbh of all these trees were recorded (2889 trees in total, inventory 2000) and four crown radii per tree were measured (2831 trees in total in 2000). While gaps were not delimited in the field, the mapping of dead trees enabled us to assume that their vicinity would be characterized by relatively high light levels. In addition, gaps were delineated based on LiDAR data in 2018 (cf. Supplementary materials, 8.7), resulting in gap area estimates between 100 and 2116 m² and an overall gap fraction of 7% (Hobi, unpublished).

2.2. Definition of advance regeneration and classification of host trees

All saplings (6.0–10.0 cm dbh) and poles (10.1–25.0 cm dbh), jointly called ‘advance regeneration’ henceforth, were chosen based on the measured dbh-height relationship. Young trees with a dbh threshold ≤ 25 cm have a maximum height of 23 m and are not reaching the canopy in the Uholka forest where *Fagus sylvatica* can reach a height of at least 50 m. Advance regeneration was spatially related to canopy (host) trees (>25 cm dbh including dead standing trees). For this, the position of all canopy trees (focal points) was linked to saplings and poles with the method of k-nearest neighbours (k = 20) based on Euclidian distances (R, package *FNN*, Beygelzimer et al. 2019). For the linked advance regeneration (Fig. 1), we applied a distance filter (crown radius + 3 m) to select only those trees located within the modelled crown radius (cf. eq. (1) of a host tree. The buffer was added to ensure that even for the smallest crown radius, the probability of random zeros (i.e., young trees are not sampled) was minimized. When counting advance regeneration per host tree, each individual was counted only once by assigning it to the closest host tree. In addition, mature dead and living neighbours of host trees were identified with the same methods as explained above (k = 20, crown radius + 3 m buffer as a cut-off). If a tree did not host advance regeneration at all, the count of advance regeneration was set to zero for each species and dbh class (saplings 6.0–10.0 cm and poles 10.1–25.0 cm). We excluded stand-alone advance regeneration (or advance regeneration cohorts) with no host tree from the model as their focal points (if any) most probably would be lying, decomposed or disappeared dead trees for which we could not model a crown radius.

All new standing dead trees (>25 cm dbh, Yamamoto 1996, Nagel et al. 2010) that appeared in any given inventory except for the inventory in 2000 (when we did not know for how long they had been dead) were considered as background mortality. This included trees that had died because of biotic causes and either remained standing with an intact crown or still had a trunk with main branches. Standing hosts found dead in a former inventory did not qualify as hosts in subsequent inventories anymore, i.e. dead standing trees were unique per inventory. Lying dead trees that had been uprooted (probably due to windstorm) were not included in the model, as they cannot be considered as background mortality (Larson and Franklin 2010). We repeated the above-

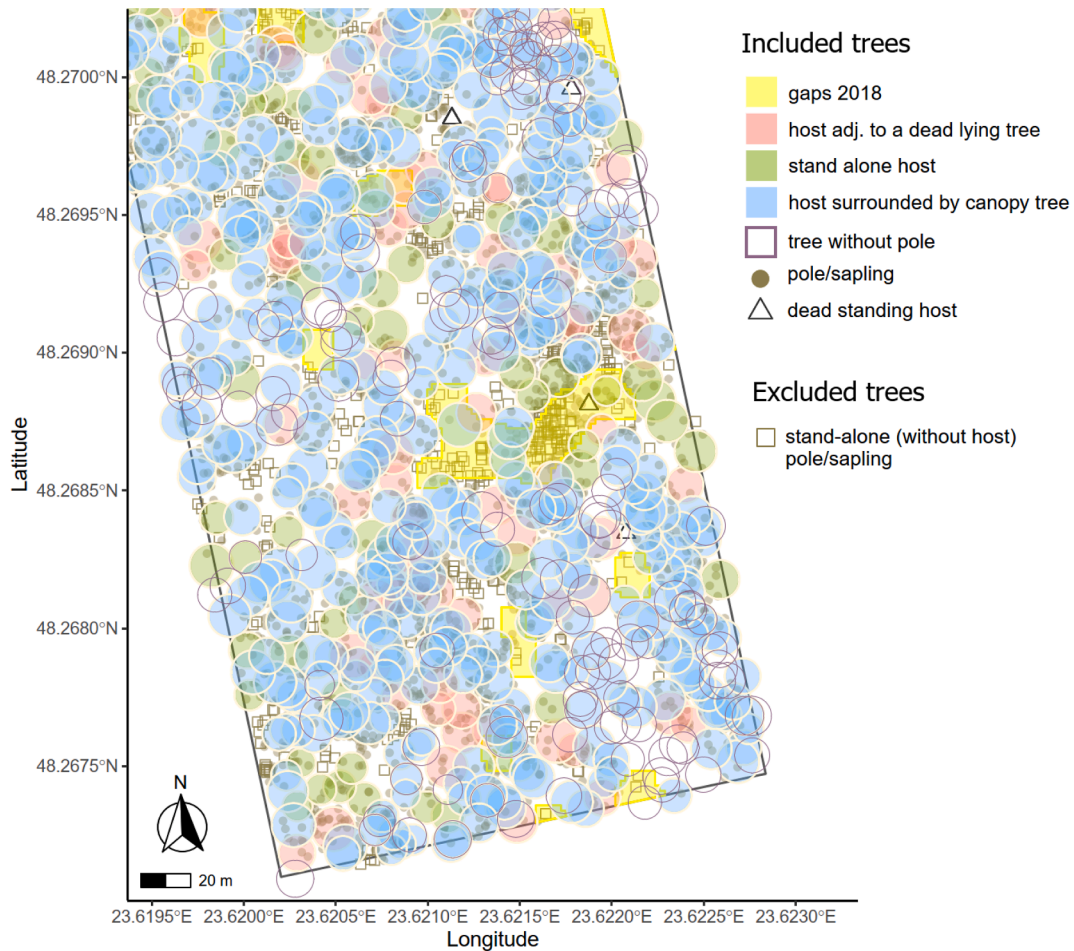


Fig. 1. Spatially related advance regeneration (saplings and poles) and host trees (diameter of circles corresponds to their crown areas) on a fragment of the 10 ha plot. Selected and excluded trees are shown for the inventory 2015 (as an example). Mapped canopy gaps based on LiDAR data of the year 2018.

mentioned procedure for each inventory (2000, 2005, 2010 and 2015).

As gaps had not been delineated for every inventory, we were unable to determine whether they had existed before 2018, the year for which we had LiDAR data. Therefore, the host trees were classified according to their neighborhood in four classes: i) host in canopy (if all neighbours were living canopy trees); ii) host adjacent to a standing dead tree if at least one standing dead tree (>25 cm dbh) was present, or iii) host adjacent to a lying dead tree if at least one lying dead tree (>25 cm dbh) was found within the modelled crown radius (plus 3 m buffer) of the host tree; and iv) stand-alone host, if there were no other living canopy trees or dead neighbours within the crown radius (plus 3 m buffer), which may occur in gaps (Fig. 1). Selected and excluded trees are shown for the inventory 2015, along with gaps identified in 2018 based on LiDAR data to verify the classification of stand-alone advance regeneration without a host (cf. Fig. 1).

3. Statistical analysis

3.1. Modelling tree crown radius

Generalised linear models for the gamma distribution with a logarithmic link function (R, package *rms*, Harrell, 2020) were applied to model the tree crown radius cr :

$$\ln(E(cr)) = \beta_0 + \beta_1 \ln(dbh) + \beta_{2,1} species_1 + \beta_{2,2} species_2 + \beta_{2,3} species_3 + \varepsilon \quad (1)$$

where E denotes expectation, β_0 = intercept, β_1 = coefficient of the

covariate, and $species_{1,2,3}$ are three indicator (dummy) variables $\beta_{2,1-2,4}$ for the four tree species, ε = random error term assumed to follow a standard normal distribution. The model assumed a linear relationship between the predictors and the link function. The statistical significance of the model coefficients was evaluated with the Wald Chi-squared test ($p < 0.01$) and additionally checked by means of bootstrapping (1000 iterations). The model satisfied the assumptions of linearity between the predictors and the link function and showed no multicollinearity (variance inflation factor VIF cut-off set at 5). The root mean square error (prediction error) was 1.25 m (31%).

3.2. Abundance of advance regeneration

A Bayesian hurdle Poisson model was used to estimate the mean number of advance regeneration per host tree (R, package *brms*, Bürkner 2020). The Bayesian approach works well with small samples, which occurred in the case of *Acer* spp. and *Ulmus glabra* in our analysis, and converges well using the gradient-based Hamiltonian Monte-Carlo sampler (Hoffman and Gelman 2014). A hurdle model accounts for structural zeros related to ecological restrictions (Blasco-Moreno et al. 2019) and it assumes that zeros and positive observations are generated by two distinct processes. Structural zeros in our study can occur due to a variety of factors such as advance regeneration not being present due to insufficient light levels, the general rarity of a species, high browsing, or low seed availability. The abundance of advance regeneration, however, is controlled mainly by species-specific mortality due to long-term shading that suppresses growth, and disturbance-related mortality. The hurdle model has two parts: 1) a binary part that captures the

absence/presence of advance regeneration with a response variable (y) as the probability of saplings or poles being absent ($y = 0$) or present (non-zero) based on a logit regression; and 2) a count part that models the estimated number of living advance regeneration ($y > 0$) as a left-truncated Poisson regression. If saplings/poles are absent, the threshold ('hurdle') to the truncated count part is not crossed, and a zero is modelled. Otherwise, the hurdle to the truncated count part is crossed, and the amount of advance regeneration is modelled (cf. [McElreath and Koster 2014](#)). The parameter p_i indicates the probability of a zero value, and μ_i is the mean of non-zero outcomes. Then, the Poisson hurdle model is defined as:

$$f(y_i) = \begin{cases} (1 - p_i) \text{Poisson}(\mu_i), & \text{if } y_i > 0, \text{ counts part of the model} \\ p_i, & \text{if } y_i = 0, \text{ absence part of the model} \end{cases} \quad (2)$$

The presence/absence probability p_i was modelled as a linear combination of (1) the continuous predictor 'crown radius of the host tree' and the factorial predictors 'sapling/pole species' ($p.sp$, total 4 species), 'subplot' (40 subplots), 'inventory year' (4 inventories) and 'host tree ID' (tree, on average 600 trees per inventory) using a logit link (eq. (4)). Here, host tree ID was used as a random effect because saplings/poles are nested under host trees. The ID of the host tree and the subplot-year interaction were used as random intercepts, allowing for correlation between year effects of the same subplot in both linear predictors. The counts μ_i are linearly connected via a log link and contain continuous predictors of stem diameter and factorial predictors including 'sapling/pole species' ($p.sp$), 'sapling/pole diameter class', and the 'neighborhood classification of their host tree' ($neighb$, 4 classes, see Methods), 'subplot', 'year', and 'host tree ID' (eq. (5)). The multicollinearity of crown radius and host dbh in either the count or logit part of the model was the main reason why we splitted these variables. In addition, the effect of host dbh on the abundance of advance regeneration is more straightforward to interpret, and thus we included 'host dbh' in the count part. We also tested in the model whether species identity of the host trees could improve the modelling results. However, no species was significant. Moreover, adding this variable did not improve the model due to the low number of host trees for *Ulmus glabra* (2 trees) and *Acer platanoides* (4 trees) ([Table 1](#)).

If we set $p.sp_i (i = 1, \dots, 4)$, $neighb_k (k = 1, \dots, 4)$, $year_l (l = 1, \dots, 4)$, $subplot_m (m = 1, \dots, 40)$, $tree_n (n = 1, \dots, 600)$, then the multi-level model formulae are:

$$f(y_{ijklmn}) = \begin{cases} (1 - p_{ijklmn}) \text{Poisson}(\mu_{ijklmn}), & \text{if } y_{ijklmn} > 0 \\ p_{ijklmn}, & \text{if } y_{ijklmn} = 0 \end{cases} \quad (3)$$

$$\text{logit}(p_{ijklmn}) = \gamma_0 + \gamma_1 \text{radius}_{ijklmn} + p.sp_i + year_l + c_{lm} + d_{n(jm)} \quad (4)$$

$$\ln(\mu_{ijklmn}) = \beta_0 + \beta_1 dbh_{ijklmn} + p.sp_i + dbh - class_j + neighb_k + year_l + a_{lm} + b_{n(jm)} \quad (5)$$

where a_{lm} , $b_{n(jm)}$, c_{lm} and $d_{n(jm)}$ denote random effects with the following correlation structure:

$$\begin{pmatrix} a_{11} \\ \vdots \\ a_{41} \\ \vdots \\ a_{140} \\ \vdots \\ a_{440} \\ \vdots \\ b_1 \\ \vdots \\ b_{600} \end{pmatrix} \sim \mathcal{N} \left(\begin{pmatrix} 0 \\ \vdots \\ 0 \end{pmatrix}, \begin{pmatrix} I_m \otimes \Sigma & 0 \\ 0 & I_m \sigma_b^2 \end{pmatrix} \right) \text{ with } \Sigma = \begin{pmatrix} \sigma_{a_{1m}}^2 & \dots & \sigma_{a_{1m}} \sigma_{a_{lm}} \rho_{a_{1m}, a_{lm}} \\ \vdots & \ddots & \vdots \\ \sigma_{a_{1m}} \sigma_{a_{lm}} \rho_{a_{1m}, a_{lm}} & \dots & \sigma_{a_{lm}}^2 \end{pmatrix} \quad (6)$$

and similarly for c_{lm} and $d_{n(jm)}$. The random effects are assumed to come from a multivariate normal distribution $\mathcal{N}$ with a mean of zero, Σ is the covariance matrix with diagonal elements of standard deviation σ , and I_m is the identity matrix.

Weakly informative priors were applied to the intercepts β_0 , γ_0 and the coefficients β_1 , γ_1 that follow a normal distribution $\mathcal{N}(\mu, \sigma^2)$ with mean μ and variance σ^2 . Weakly informative priors are preferable in the case of small samples ([McNeish 2016](#)) and restrict the parameter values to a reasonable range without strongly influencing the posterior distribution ([Lemoine 2019](#)). A half-t distribution (half-student distribution) with 4 degrees of freedom, mean and scale was applied for the intercepts and the standard deviations of the group levels ([Gelman 2006](#)):

$$\begin{aligned} \beta_0 &\sim \text{half} - t(4, 0, 1) & \sigma_{a_{lm}} &\sim \text{half} - t(4, 0, 0.5) \\ \beta_{1,2} &\sim \text{normal}(0, 0.3) & \sigma_{b_{n(jm)}} &\sim \text{half} - t(4, 0, 0.5) \\ \gamma_0 &\sim \text{half} - t(4, 0, 0.5) & \sigma_{c_{lm}} &\sim \text{half} - t(4, 0, 0.5) \\ \gamma_1 &\sim \text{normal}(0, 0.5) & \sigma_{d_{n(jm)}} &\sim \text{half} - t(4, 0, 0.5) \end{aligned}$$

Additionally, to better understand the impact of the priors on the posterior results, we estimated the relative bias of the parameters for models with weakly informative vs. non-informative priors. In a sensitivity analysis, the mean of the weakly informative priors was varied upward and downward by 0.1. The model with non-informative priors had issues with multicollinearity, while the statistical findings from models with weakly informative priors were comparable for all models. This indicates that the parameter estimation was driven by the properties of the data rather than the nature of the priors.

The model fully converged and stabilized ($\hat{R} \leq 1$, [Gelman and Rubin 1992](#)) after running on 4 chains and with 4,000 iterations per chain plus 1000 iterations for warm-up. It did not show autocorrelation in the chains (cf. [Supplementary material](#)). A relatively high effective sample size (ESS, [Table 2](#)) highlighted the ability of the draws to estimate the true mean values of the parameters ([Gelman et al. 2013](#)). The predictive accuracy of the posterior distribution was estimated with approximate

Table 1

Samples of living host trees, living saplings and poles under host trees, and host trees without saplings and poles (all included in the model) relative to the total number of trees on the 10 ha plot (after /) per inventory. The mean dbh and crown radius of the host trees with standard deviation (sd) are given per species. Species: *A. platanoides* (A. pla), *Acer pseudoplatanus* (A. pse), *Fagus sylvatica* (F. syl), *Ulmus glabra* (U. gla).

Category	Species	N'00/ total	N'05/ total	N'10/ total	N'15/ total	dbh $\pm$ sd [cm]	Crown radius $\pm$ sd [m]
Host trees (dbh > 25 cm)	A. pla	4 / 6	5 / 6	5 / 6	6 / 7	48.3 (15.4)	4.5 (0.6)
	A. pse	18 / 36	16 / 35	19 / 35	30 / 35	56.8 (15.5)	4.8 (0.5)
	F. syl	591 / 1,119	617 / 1,073	677 / 1,007	802 / 989	63.5 (22.4)	5.7 (0.8)
	U. gla	2 / 3	2 / 3	1 / 3	2 / 3	49.6 (10.4)	5.7 (0.5)
Saplings/poles under host (dbh 6–25 cm)	A. pla	4 / 7	4 / 8	20 / 26	185 / 217	8.2 (3.5)	
	A. pse	6 / 8	9 / 18	29 / 44	129 / 212	8.0 (2.6)	
	F. syl	1,437 / 1,604	1,542 / 1,729	1,825 / 2,034	2,835 / 3,115	10.8 (4.4)	
	U. gla	4 / 5	6 / 7	15 / 16	87 / 104	8.8 (2.6)	

Table 2

Results of the hurdle Poisson model indicating the number of tree regeneration in the counts part (right) and the likelihood of its presence in the logit part (left). Incidence rate - exponentiated coefficients, sd – standard deviation, %in ROPE [full] - percentage in ROPE as an index of significance, ESS – effective sample size, AR – advance regeneration, A. pla – *A. platanoides*, A. pse – *Acer pseudoplatanus*, F. syl – *Fagus sylvatica*; Bayesian significance is marked as (*). Total number of observations: 4,275.

Parameter	Odds ratio(sd)	% inROPE [full]	$\hat{R}$	ESS	Incidence rate (sd)	% inROPE [full]	$\hat{R}$	ESS
Logit part					Counts part			
Intercept	0.01 (1.82)	0.0*	1.0	10,310	0.44 (1.15)	0.0*	1.0	9,290
Host dbh [cm]					1.04 (1.15)	65.7	1.0	20,394
Host crown radius [m]	0.83 (1.6)	43.1	1.0	12,187				
A. pla (AR)		reference				reference		
A. pse (AR)	1.24 (1.56)	40.3	1.0	10,707	1.29 (1.15)	14.3	1.0	22,837
F. syl (AR)	0.47 (1.58)	7.5*	1.0	9,725	1.76 (1.11)	0.0*	1.0	24,129
U. gla (AR)	1.29 (1.57)	35.9	1.0	10,178	0.56 (1.19)	0.2*	1.0	19,529
Dbh class of AR						reference		
[10.1–25.0 cm]								
[6.0–10.0 cm]					1.19 (1.03)	2.0*	1.0	8,209
Host adj. lying dead						reference		
Host adj. dead standing					0.81 (1.22)	29.8	1.0	17,745
Host in canopy					0.93 (1.06)	68.2	1.0	10,544
Host standing alone					1.40 (1.09)	0.3*	1.0	9,807
Inventory 2000		reference				reference		
Inventory 2005	1.00 (1.56)	57.8	1.0	8,512	0.98 (1.06)	92.4	1.0	25,981
Inventory 2010	0.83 (1.65)	43.4	1.0	7,885	1.11 (1.06)	52.0	1.0	16,048
Inventory 2015	0.83 (1.68)	43.1	1.0	8,021	1.60 (1.07)	0.0*	1.0	10,126

* Note: Bayesian statistical significance is not directly comparable to significance in frequentist statistics.

leave-one-out cross-validation (LOO) based on Pareto-smoothed importance sampling (Vehtari et al. 2017). Model choice was based on the highest expected log predicted density (elpd_loo) and the lowest LOO Information Criterion (looic). The Pareto k-values did not exceed 0.6 without influential observations (cf. Supplementary material).

In Bayesian inference, goodness-of-fit is evaluated via posterior simulations, i.e. new data are simulated from the model with parameters from the estimated posterior distributions, and the simulated data are compared to the observed data. Therefore, we simulated new data based on 2000 draws from the parameters' posterior distribution and compared the mean and standard deviation with the observed data (cf. Supplementary material). Model residuals were approximately normally distributed, random effects followed a normal distribution, and covariates showed no multicollinearity. The model showed no over-dispersion either. The significance of the effects was tested with the full region of practical equivalence ROPE [full] (Kruschke 2018) based on high-density intervals (HDI). Values of the distribution both below and above the ROPE (−0.1, 0.1) indicate practical significance (Kruschke 2018; Makowski et al. 2019).

4. Results

4.1. Samples of host trees and spatially related saplings and poles

In the 2000 and 2005 inventories, only half of the host trees were spatially associated with advance regeneration. In contrast, in the 2015 inventory, 81% of the host tree population was spatially associated with saplings or poles due to high ingrowth under host trees (Table 1). The storms in 2007 and 2009 had created gaps, thus allowing more light to penetrate below the canopy and raising the number of new saplings in the time between the inventories of 2010 and 2015. Advance regeneration under the host trees represented almost the entire population of saplings and poles, with only about 10% of the juvenile trees standing alone or as cohorts in gaps. In short, the sample consisted of most of the host trees and advance regeneration population on the 10 ha plot.

Fagus sylvatica featured a steady proportion of the number of advance regeneration to the number of host trees during the inventories 2000–2010 but showed a substantial increase in 2015 (Table 1). In contrast, *Acer* spp. had a negligible number of saplings and poles in 2000 and 2005, but after the storms their number went up strongly for the inventories of 2010 and 2015.

Surprisingly, most *Fagus sylvatica* poles appeared under *Acer* spp. or *Ulmus glabra* hosts while *Acer* spp. and *Ulmus glabra* poles grew mostly under *Fagus sylvatica* hosts (Fig. 2). In 2000, almost all *Acer* spp. hosts were occupied by *Fagus sylvatica* poles, and similar pattern was found in 2015. Comparing the inventories of 2000 and 2015, hosts in higher dbh classes (>85 cm) accumulated more poles of *Fagus sylvatica* with time or/and with higher light availability, while *Acer* sp. and *Ulmus glabra* poles competed more successfully among hosts in the lower dbh classes (<85 cm).

A closer look at the location and neighborhood of trees without advance regeneration revealed that they were growing mostly in dense clusters around dead lying trees in the inventory 2005. These clusters created patches with low light availability and thus suppressed regeneration. However, after two windfalls some of these trees were killed, thus allowing for more light that triggered rapid sapling recruitment. Subsequently, most trees without advance regeneration became hosts in 2015 inventory.

The number of *Fagus sylvatica* stand-alone poles growing, presumably, in gaps (cf. Fig. 1) increased in 2010–2015 (Fig. 3A). The rates of increase in saplings were quite similar for *Fagus sylvatica* and *Acer pseudoplatanus* but much lower at the pole stage for the latter. Interestingly, *Acer platanoides* was able to produce a similar number of saplings and poles as *Acer pseudoplatanus* in spite of much fewer mother trees although we did not know the number of seed trees outside of 10 ha plot (Table 1, Fig. 3A).

Only some gaps delineated by LiDAR in 2018 contained advance regeneration without hosts (Fig. 3B). It is noteworthy that the k-nearest neighbour method identified more gaps with stand-alone regeneration than LiDAR-derived gaps, but their size was impossible to determine. The number of saplings and poles in small gaps (<296 m²) appeared to be negligible, but the amount of advance regeneration substantially increased in gaps > 552 m². Saplings of *Acer pseudoplatanus* by far outcompeted *Fagus sylvatica* while keeping the same number of poles as dominant species in the gap size class 2116 m².

4.2. Sapling and pole abundance as an indicator of host replacement

In the hurdle model, the count and survival parts are separated, thus allowing the coefficients of the relationship between the predictor variables and the abundance of advance regeneration to be interpreted easily. An increase in one unit of host dbh (i.e., by 1 cm) increased the

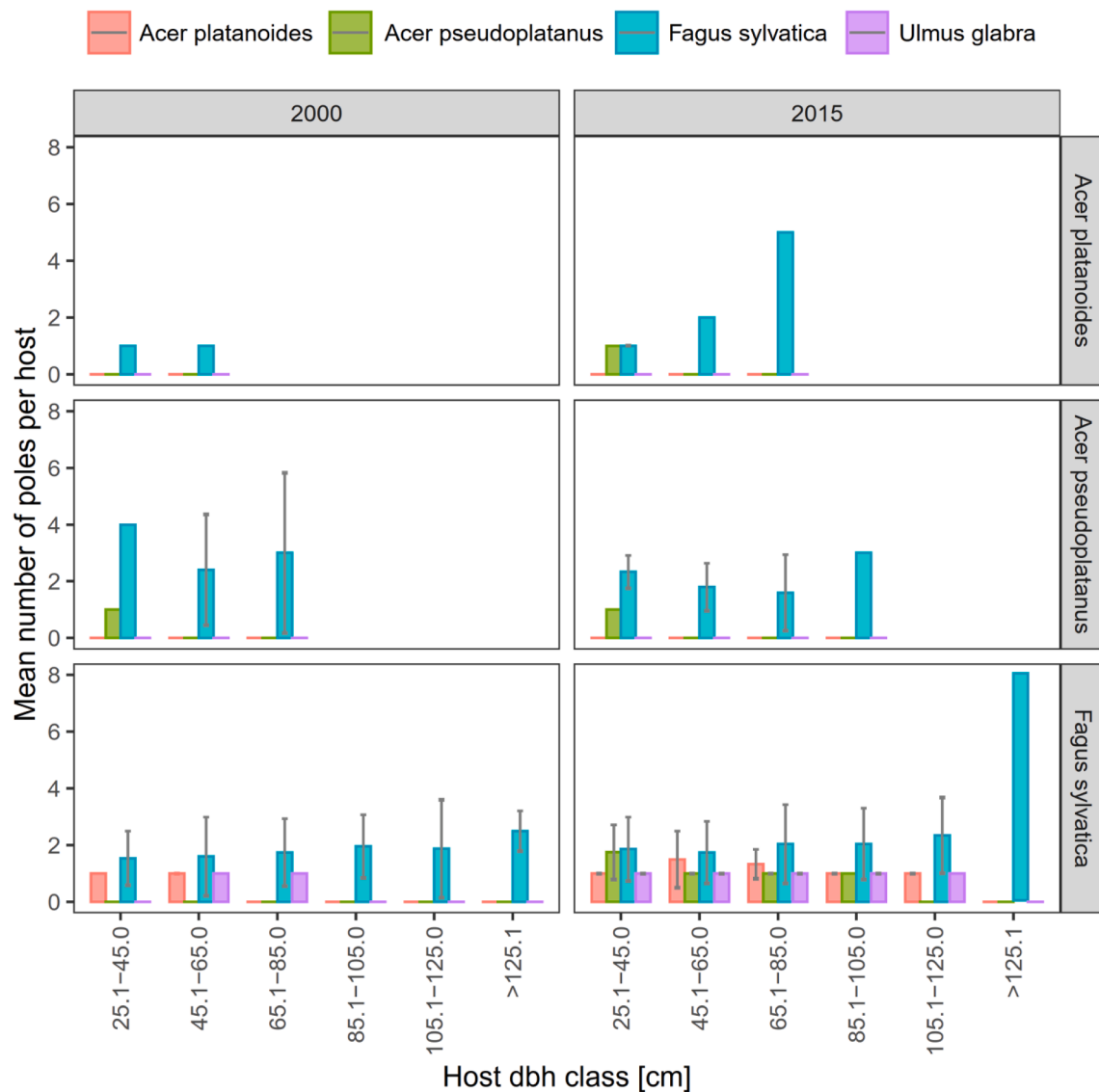


Fig. 2. Mean number of poles (10.1–25.0 cm dbh) per host diameter class and host species (by row). Whiskers indicate one standard deviation. Note: two host trees of *U. glabra* were omitted here for readability.

mean number (incidence rate) of advance regeneration by 1.04 points (cf. Table 2), respectively, for the same inventory period and subplot when holding the other covariates constant. This effect was not significant because the credible intervals were inside the ROPE indicator (see % inROPE [full], Table 2). When holding the other covariates constant, the mean number of advance regeneration was 1.29 points higher in *Acer pseudoplatanus* than in *A. platanoides* for the same year and subplot (difference not significant), while the number was significantly higher in *Fagus sylvatica* advance regeneration (by 1.76 points) and lower in *Ulmus glabra* (by 0.56 points).

As expected, stand-alone hosts recruited the largest number of saplings and poles due to the high light levels (significant effect), while trees in the vicinity of a standing dead tree or those that were surrounded by other living canopy trees were less likely to host advance regeneration compared to hosts adjacent to lying dead trees. Nevertheless, despite the high impact of stand-alone hosts on the recruitment of young trees, hosts adjacent to lying dead trees were found to recruit advance regeneration at a higher rate. For example, the number of young trees under hosts adjacent to lying dead trees changed from 78 to 486 trees in 2000 vs. 2015, while for stand-alone hosts the rate of change was less pronounced, i.e. from 276 to 351 trees for the same period. The model

predicted an increase in the mean abundance of advance regeneration compared to the 2000 inventory for the inventories after the storms in both 2010 (by 1.1 points, not significant) and 2015 (by 1.6 points, significant).

In the logit part of the model (Table 2), an increase in the crown radius of a host tree by one unit led to a decrease of the adjusted odds of advance regeneration to be absent by a factor of 0.83 for the same year and subplot. Compared to *A. platanoides*, advance regeneration of both *Acer pseudoplatanus* and *Ulmus glabra* had lower chances to be hosted than that of *Fagus sylvatica*. Due to improved light conditions after the windstorms, the likelihood of advance regeneration being absent decreased in 2010–2015 compared to 2000, confirming the similar effect in the counts part of the model (Table 2).

Generally, the number of advance regeneration hosted under trees in different neighborhoods was slightly lower for poles (Fig. 4A) than for saplings (Fig. 4B) due to self-thinning effect. The proportion of saplings to poles (i.e. 1.1:1) was nearly constant since 2000 and even nearly 1:1 in 2010 due to disturbance mortality, whereas after two windfalls it increased to 1.5:1 in 2015. Also, there was a clearly higher number of advance regeneration under hosts with increasing diameter. The availability of poles under hosts in different host neighborhoods and in

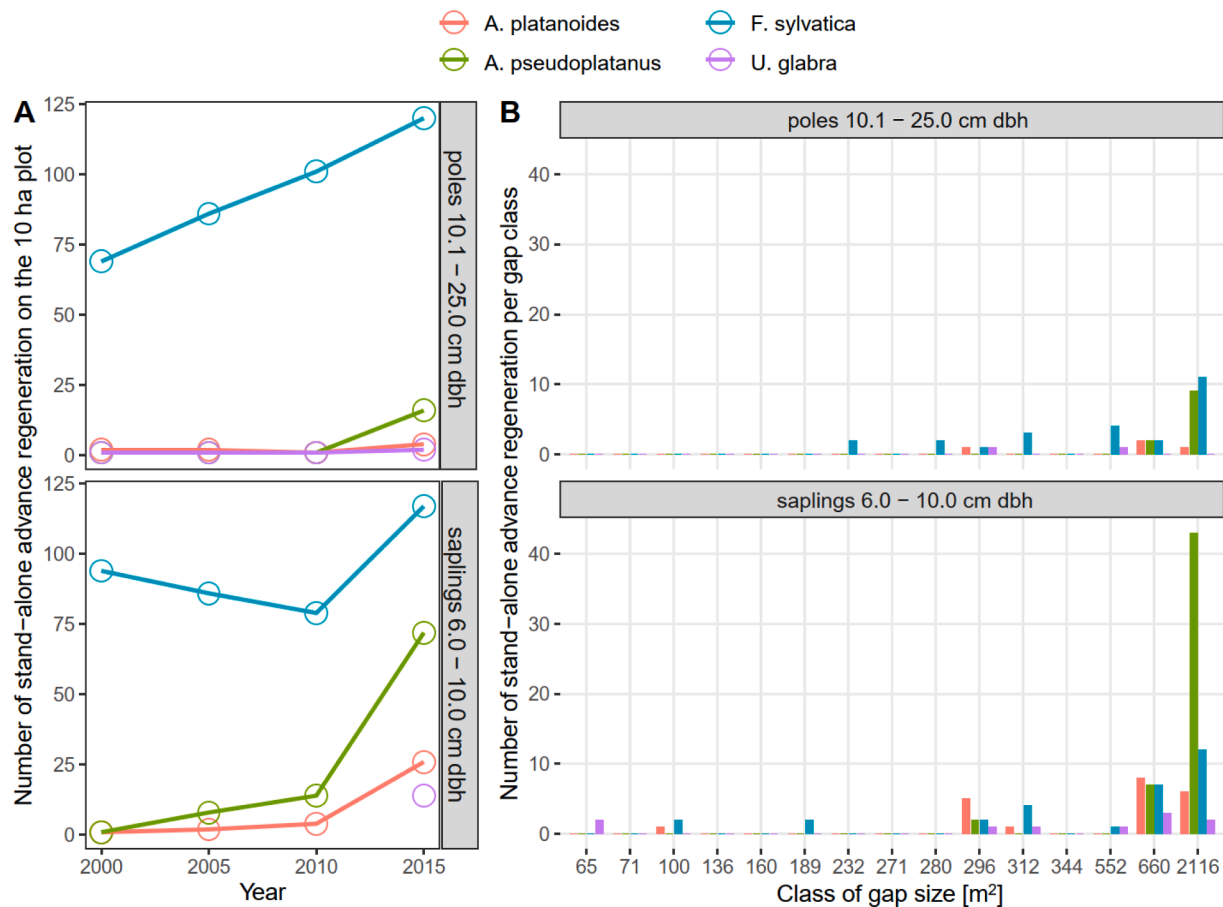


Fig. 3. A: total number of stand-alone, i.e. host-free, saplings (dbh 6.0–10.0 cm) and poles (dbh 10.1–25.0 cm) in the four inventories 2000, 2005, 2010, 2015 on the 10 ha plot; B: advance regeneration in gaps delineated in 2018.

dependence of host dbh mirrored the presence of saplings, but at clearly lower levels (Fig. 4A). At host dbh 40 cm, the number of *Fagus sylvatica* poles in shaded conditions (i.e., host in canopy) was low (mean = 0.6, CI [0.4, 0.8]) and increase to one pole under hosts > 80 cm dbh. The abundance of poles and saplings under hosts adjacent to dead standing trees was similar to those for the hosts in the canopy (data not shown). Light availability for hosts adjacent to dead standing trees was too low to promote a pole or sapling of *Acer* spp., but sufficient to recruit one pole of *Fagus sylvatica* under a host > 80 cm dbh. Moreover, hosts in the vicinity of dead lying trees or stand-alone hosts showed an intermediate abundance of *Fagus sylvatica* poles (mean = 0.9 and 1.2), suggesting realistic chances for a successful replacement. Unlike in *Fagus sylvatica*, the low numbers of *Acer* spp. and *Ulmus glabra* poles in shaded conditions most likely render replacement a rare event. Only near a dead lying tree, *Acer pseudoplatanus* hardly achieved an abundance of one pole at host dbh values > 80 cm. Finally, in gaps both *Acer* spp. were able to compete to a certain degree with *Fagus sylvatica* poles (Fig. 4A).

Under low light levels (i.e., host in canopy), one sapling of *Fagus sylvatica* (mean = 0.96, CI [0.8, 1.1]) was present as a potential replacement for one host of 60 cm dbh, or for one host adjacent to a dead lying tree (mean = 1.0, CI [0.9, 1.2]; Fig. 4A). If a host was in gap (stand-alone host), up to two *Fagus sylvatica* saplings were available as potential replacement for hosts with a dbh > 60 cm. The number of saplings potentially replacing a host was lower in *Acer pseudoplatanus* than in *Fagus sylvatica*, and close to 1 only if the host was large (dbh > 60 cm), either in the vicinity to a dead canopy tree or standing alone in a gap (mean = 1.1, CI [0.8, 1.4]). In contrast, at these locations neither *Acer platanoides* nor *Ulmus glabra* seem able to recruit a sapling for replacement of a host (60 cm dbh), although proximity to a gap increased the

chances for replacement in *Acer platanoides* saplings (mean = 0.8, CI [0.6, 1.1]).

5. Discussion

5.1. Replacement of canopy trees

We studied the frequency of potential recruits to the canopy under hosts, not recruiting events over time. However, we were able to infer from the number of recruits under a host whether a replacement is likely to occur in case the host dies. A higher number of recruits of a given species under a host makes an actual replacement more likely, and vice versa. The number of poles per host in the model is a reasonable predictor for the actual number of replacement events, whereas the number of saplings is likely to be less reliable, because a lot can still happen until these saplings become poles. Unlike previous studies (e.g., Busing 1996; Nagel et al. 2010), we did not assume that the presence of one successor sapling/pole underneath a host tree suggests that this sapling/pole will indeed replace the host. Instead, we accounted for the population of all saplings and pole-stage trees, thus yielding a more accurate estimation of the successor species based on Bayesian statistics. On this account, our study is close to Horn's (1975) model where the proportion of saplings under a host tree was used to derive the probability of replacement. The quality of Bayesian inference (McNeish 2016) about model parameters is not controlled by sample size, as in frequentist statistics (i.e., a small sample implies a high bias), but rather by the number of samples simulated (ESS in Table 2). The simulated effective samples were sufficient to draw conclusions on replacement rates not only for the dominant species *Fagus sylvatica*, but even for the minor species *Acer*

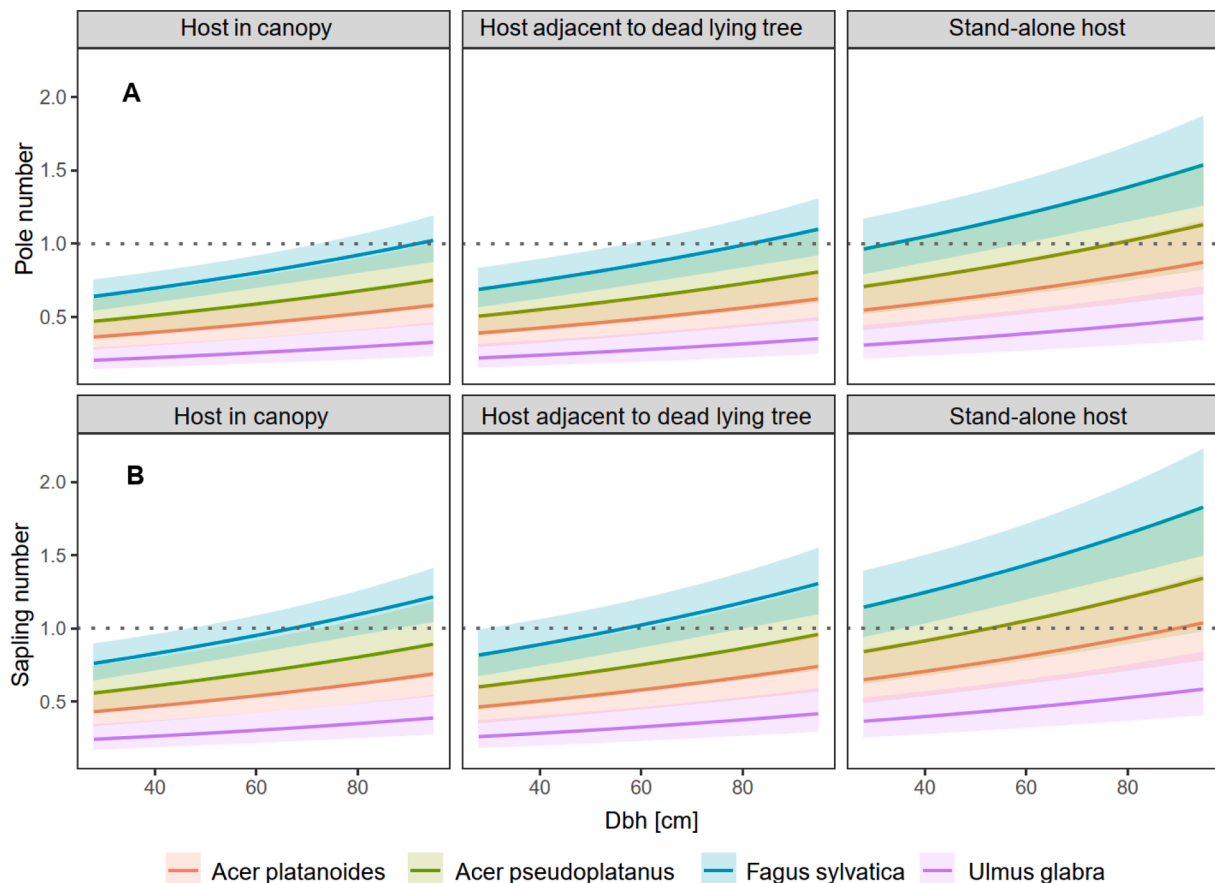


Fig. 4. A: Number of poles (dbh 10.1–25.0 cm) and B: saplings (6.0–10.0 cm) under a host tree in different host neighborhoods. Thick lines are marginal means averaged for the four periods, shaded regions 95% credible intervals (CI) for the marginal means, and the grey dotted horizontal line indicates the threshold for potential replacement by at least one pole. Note: abundance of advance regeneration under a host tree adjacent to dead standing tree is similar to a host in canopy and is not presented.

spp. and *Ulmus glabra*. The hurdle model assumes that two processes, i.e. i) the presence of advance regeneration and ii) its abundance are taking place separately. The presence of saplings is governed primarily by the seed availability (Kolo et al. 2017), light levels (canopy opening 7%) and browsing. Indeed, all four inventories on the 10 ha plot show that juveniles of *Acer* spp. (≥ 130 cm height and up to 6 cm dbh) compete successfully with *Fagus sylvatica*, indicating that species-specific mortality due to differences in shade tolerance plays a less important role at these light levels (unpublished data). On the contrary, the abundance of advance regeneration is controlled primarily by species-specific mortality due to long-term shading (Brüllhardt et al. 2022) and disturbance-related mortality when a pole gets snapped by a host or uprooted by abiotic disturbance (Nagel et al. 2021).

Our study provides no indication of reciprocal canopy replacement between *Fagus sylvatica* and *Acer* spp. or *Ulmus glabra*, as was observed between *Fagus sylvatica* and *Abies alba* poles (Nagel et al. 2010), between *Fagus sylvatica* and conifer species (Keren et al. 2014), or between *Fagus grandifolia* and *Acer saccharum* (Poulson and Platt 1996; Woods 1984) in North America. Similar to European *Acer pseudoplatanus*, *Acer saccharum* is considered less shade-tolerant species than *Fagus grandifolia* (Beaudet et al. 1999; Beaudet and Messier 1998; Canham 1988; Collin et al. 2017; Kobe et al. 1995), however it shares dominant position with the latter due to higher frequency and larger scale of disturbance in North America compared to Europe (Marshall and Camp 2013). Reciprocal replacement of *Abies alba* and *Fagus sylvatica* was explained by gap size, i.e. the former was able to reach the top canopy in small and mid-sized gaps while the latter occurred mainly in gaps > 400 m² (Nagel et al. 2010). In this study, the ratio of mature *Fagus sylvatica* trees to poles was similar, i.e.

2.3 poles/tree vs. 2.4–3.5 poles/tree (inventories 2000–2015, Table 1), but distinctly higher for *Acer pseudoplatanus*, i.e. 6 poles/tree vs. 0.3–4 poles/tree for the same time period. Despite a higher number of *Acer pseudoplatanus* poles per mature tree than in our study, Nagel et al. (2010) estimated the chance of this species to replace mature *Fagus sylvatica* as 4%. A comparable study in North America reported a similar proportion for *Fagus grandifolia*, i.e. 2.1 poles (5–12.5 cm dbh) per tree (> 20 cm dbh), and for *Acer saccharum* 4 poles/tree, albeit with reciprocal replacement of species (Woods 1979). Given the fact that all these studies were cross-sectional, a proportion is not a reliable estimate of tree replacement probability without additional information on the dynamics in advance regeneration and the disturbance regime. We found competitive replacement of heterospecific host trees by *Fagus sylvatica* advance regeneration (Fig. 2) irrespective of the neighborhood (Fig. 4), whereas the self-replacement of *Acer* spp. occurred only in the proximity of lying dead trees, and for *Ulmus glabra* in gaps. Hence, given the prevailing single-tree mortality in our study area and the gap fraction (currently 7%), canopy replacement benefits mostly *Fagus sylvatica*.

In previous research, the probability of replacement was typically derived from cross-sectional rather than longitudinal data (Fox 1977; Nagel et al. 2010; Poulson and Platt 1996; Woods 1984). In our study, other uncontrolled factors such as wet snow and browsing can limit recruitment to advance regeneration. For example, *Acer* spp. regeneration is easily bent under heavy snow (Hein et al. 2009) and often cannot resume vertical growth. In addition, ungulates selectively browse *Acer* spp. and *Ulmus glabra* (Ammer 1996; Schulze et al. 2014), and browsing pressure on the 10 ha plot varies from one inventory period to the next. Therefore, we used a longitudinal study instead of a cross-sectional one

to account for undetected changes in these factors at the subplot and host level. We allowed for correlation between year effects of the same subplot in both linear predictors, which is why the number of advance regeneration available for replacement and also their absence differed between periods (Table 2). We found that the number of advance regeneration under a host significantly increased during the inventory period 2010–2015, especially in the vicinity of dead lying trees and gaps. However, between 2010 and 2015 the number of host trees increased substantially as well, maintaining a similar amount of advance regeneration per host as before.

The stand structure on the 10 ha plot studied here differs from that of the entire reserve, e.g., the 10 ha plot has higher basal area, host tree diameters (Peck et al. 2015), abundance of small saplings (up to 1.3 m in height) of *Acer* spp. and *Ulmus glabra* (Commarmot et al. 2005; Stillhard et al. 2019), and a higher gap fraction (Hobi et al. 2015). Nevertheless, neither the high gap fraction nor the higher frequency of windfalls stimulated significant recruitment to poles of *Acer* spp. and *Ulmus glabra* compared to *Fagus sylvatica* stand-alone advance regeneration on the 10 ha plot (Fig. 3). Stillhard et al. (2022) reported a 97% share of *Fagus sylvatica* in the sapling class (0–5.9 cm dbh) for the entire Uholka-Shyrokiy Luh reserve. This suggests that replacement on the 10-ha plot occurs mostly under the single-tree mortality scenario (Fig. 4) and follows the same pattern as in the entire reserve, thus explaining the strong *Fagus sylvatica* dominance in this forest.

5.2. Factors affecting replacement

We studied two situations of tree-by-tree replacement: i) the replacement of canopy trees in a matrix of other living canopy trees, based on spatial associations between overstory and understory trees (Culver 1981; Fox 1977; Horn 1975; Woods 1984); and ii) the replacement of canopy trees that are adjacent to or in gaps (in the vicinity of lying dead trees or stand-alone host trees) (Lertzman 1992, 1995; Runkle 1981). Some studies (Ammer and Weber 1999; Busing and White 1997; Denslow 1995) suggested that gaps are not necessarily the primary sites of successful regeneration of shade-tolerant species. Yet, in our study the number of advance regeneration per host was higher for hosts in the vicinity to lying dead trees and gaps (Table 2), and significantly lower for hosts surrounded by neighbouring canopy trees. Our findings are thus in line with those of Feldmann et al. (2018, 2020), who reported the density of *Fagus sylvatica* saplings (≥ 0.5 m height and dbh < 7 cm) to be five times higher in gaps than under the closed canopy. However, our findings here contradict those of Nagel et al. (2010), who found that the density of *Fagus sylvatica* advance regeneration was largely decoupled from light levels. We found that host neighborhood (only living canopy trees vs. at least one dead tree vs. no neighbours, suggesting a gap) as an indicator of local light availability is pivotal for *Acer* spp. and *Ulmus glabra* as it substantially increases the recruitment of saplings to poles and, subsequently, the number of poles in higher dbh classes (Fig. 4).

In our study, the dbh of a host tree did not have a significant effect on the amount of advance regeneration underneath it, although hosts in high dbh classes accumulated advance regeneration with time (Fig. 2) and increasing light availability. Indeed, since 2007 the neighbourhood of many hosts had changed, and we assume that the additional light becoming available promoted the growth of seedlings to saplings and poles. This process went along with the ingrowth of host trees into high dbh classes. Hence, we surmise that the increase in the amount of advance regeneration under hosts in high dbh classes is related to (1) high seed productivity of hosts with large dbh, (2) processes depending on time (e.g., increasing crown senescence and disintegration), and (3) changes in host neighborhood (e.g., increasing light availability). We cannot, however, exclude an effect of the crown area geometry because trees with larger dbh have also larger modelled crown radii.

Several studies reported different relations between *Fagus sylvatica* poles and hosts of conifer and broadleaved species in old-growth

European forests. *Fagus sylvatica* poles alone were negatively spatially related to conspecific adult trees (Janík et al. 2014) and the probability of replacement of dead *Abies alba* trees by *Fagus sylvatica* poles was higher than of dead *Fagus sylvatica* trees (Nagel et al. 2010). A negative correlation between *Acer pseudoplatanus* poles and *Fagus sylvatica* hosts up to 6–7 m in distance was found by Janík et al. (2016), whereas *Fagus sylvatica* poles showed no or only a weak positive correlation to *Acer pseudoplatanus* hosts. Although we did not include host identity in the final model, one of the preliminary models was built with this explanatory variable. The amount of advance regeneration was slightly lower under *Fagus sylvatica* than under *Acer pseudoplatanus* hosts, even though this effect was not significant. Our results show that the host neighbourhood, rather than its species identity, plays a crucial role in the accumulation of poles. *Fagus sylvatica* canopy trees can host numerous heterospecific poles (Fig. 2) provided the hosts are located near dead lying trees or gaps.

We did not consider host-free advance regeneration in our analysis. Could these individuals make a difference, and in particular explain why *Fagus sylvatica* is not entirely excluding the minor species from reaching the canopy at larger scales? A similar study focusing on the analysis of sapling (< 4 cm dbh) and pole recruitment (4–12 cm dbh) after wind disturbance on permanent plots over 25 years showed that both regeneration classes of *Fagus sylvatica* successfully recruited in high amounts after disturbances while the number of *Acer* spp. saplings decreased and the number of poles lagged behind those of *Fagus sylvatica* (Scherrer et al. 2022). Although in our study the number of *Acer pseudoplatanus* saplings without hosts increased presumably in gaps (Fig. 3), they did not respond with strong growth and recruitment to poles after wind disturbances, supporting the proposition that shade negatively influences the height and diameter increment of *Acer* spp. regeneration with increasing age (Brüllhardt et al. 2020; Schmidt and Roloff 2014). This provides support to the notion that *Acer pseudoplatanus* may be able to maintain its presence in the canopy only when two circumstances coincide: i) saplings are still able to react strongly in their growth when light levels increase; ii) a canopy opening is big enough so as to provide the time required for the recruitment to pole. This suggests that *Acer* species regenerate in some pulses (Jentsch and White 2019) with low probability of the coincidence of factors mentioned above and thus of recruitment to the canopy, confirming the interpretation of the statistical model of pole number. In contrast, *Fagus sylvatica* is able to grow not only to higher dbh classes (Nagel et al. 2010) but also in higher numbers in gaps due to lower mortality in the shade compared to *Acer* spp. (Kunstler et al. 2005; Petrişan et al. 2007; Petrovska et al. 2021). The number of *Fagus sylvatica* stand-alone saplings and poles increased at a higher rate than those of *Acer* spp., and they became more numerous especially at the pole stage (Fig. 3). To conclude, gaps have an important role for long-term species coexistence, and they can become dominated by pure *Fagus sylvatica* advance regeneration (Feldmann et al. 2018; Jalovičar et al. 2020; Kramer et al. 2014), or they may harbour occasional *Acer* spp. and – even more rarely – *Ulmus glabra* advance regeneration, be it as single poles or as cohorts.

The occurrence of canopy trees that do not host advance regeneration can partly be explained by the calliper threshold. Also, the method of k-nearest neighbours assigns a sapling or pole to a host based on the nearest distance inside perfect circular crown projection, even though a pole may grow outside of its host's irregular crown projection in a real forest. Hence, the distribution of advance regeneration is more clustered for some hosts, leaving some mature trees without advance regeneration. In addition, increased mortality of poles, especially *Fagus sylvatica*, due to windthrow on the 10 ha plot was also observed in other temperate forests, where regeneration at the pole stage showed the largest decrease in density (Gabrysiak et al. 2021), and in boreal forests at a range of storm intensities (Rich et al. 2010; Shorohova et al. 2008). However, the rapid recruitment of advance regeneration in the inventories of 2015 vs 2010 suggests that its absence under some trees was mainly due to the calliper threshold and method used for the spatial identification of

host and its advance regeneration.

5.3. Management implications

The maintenance of minor broadleaved species such as *Acer* spp. and *Ulmus glabra* in stands dominated by beech is an important management question. Previous research on *Acer* spp. saplings showed their ability to survive in deep shade (mean 2–3% of diffuse light) up to 48 years (Petrovska et al. 2021). However, shade negatively influences the height and diameter increment of these species with increasing age (Brüllhardt et al. 2020; Hein et al. 2009; Mosandl and El Kateb 1988; Schmidt and Roloff 2014). Some silvicultural guidelines recommend an opening of the canopy as soon as *Acer pseudoplatanus* reaches 2–4 m in height (Leder 2009). However, already 1–2 m tall saplings growing in the shade may stagnate in height growth (Schmidt and Roloff 2014). Therefore, it is critical to open the canopy at 1–2 m sapling height to maintain *Acer* spp. at sufficient density, i.e. before their mortality sharply increases (Petrovska et al. 2021), so as to stimulate their diameter and height growth at an early age (Brüllhardt et al. 2020; Hein 2003).

Canopy openings that are as large as the crown projection of a mature beech tree ($\leq 184 \text{ m}^2$, modelled max. crown area in this study) are clearly insufficient for *Acer* spp. recruitment. In our study, a canopy opening equivalent to at least 3–4 tree crowns (about $550\text{--}736 \text{ m}^2$) strongly accelerated the recruitment of *Acer* spp. and *Ulmus glabra* saplings to poles (Fig. 3B) and increased the chances for replacement of host trees by *Acer* spp. and *Ulmus glabra* in the vicinity to gaps (Fig. 4, Brüllhardt et al. 2020). If the goal is to retain *Acer* spp. and *Ulmus glabra* poles, one should pay special attention to the often numerous advance regeneration of *Fagus sylvatica*. One option is to create canopy openings together with a thinning from below in advanced *Fagus sylvatica* saplings/poles, so as to reduce their competition in gap.

A number of recent studies demonstrated that an increase in basal area negatively influences the recruitment of advance regeneration in managed uneven-aged forests (Brüllhardt et al. 2022; Käber et al. 2021; Trifković et al. 2023). In our study, however, the number of young trees increased with host dbh, especially for *Fagus sylvatica* under host trees $> 105 \text{ cm dbh}$ (Fig. 2, Fig. 4), while basal area practically has not changed ($39.1 \text{ m}^2 \text{ ha}^{-1}$ in 2000 vs. $38.4 \text{ m}^2 \text{ ha}^{-1}$ in 2015). In old-growth beech forests (Dobroč, Badín, and Kyjov in Slovakia), the number of recruited trees (8–12 cm dbh) was not necessarily affected negatively by high basal area, and low basal area did not warrant high recruitment of advance regeneration (forests Havešová, Sitno, Stuzica, Kulla et al., 2023). Kolo et al. (2017) showed that the presence of regeneration in managed forests tends to be influenced positively by basal area (trees $> 40 \text{ cm dbh}$) and tree age, as older trees produce more seeds. Older, larger trees are often missing entirely or are at least scarce in managed forests, but they are pivotal for regeneration dynamics and the replacement process.

Due to Dutch elm disease, *Ulmus glabra* is of low interest to forest managers today, but still important for conservation as a threatened species (Thomas et al. 2018). In some mixed forests without *Fagus sylvatica*, *U. glabra* was the third most abundant species before elm disease (Puspure et al. 2016). We found that the species' pole number increased substantially in the vicinity of gaps, suggesting that it depends on the presence of larger gaps (Lygis et al. 2014), although it was found to recruit well in openings $< 200 \text{ m}^2$ in rather open boreal *Picea abies* forests (Drobyshev 2001). Taking into account the fast closure of small gaps in *Fagus sylvatica* dominated forests (Madsen and Hahn 2008), larger gaps and an early release are needed to maintain *Ulmus glabra* as well as *Acer* spp. in these forests. Consequently, single-tree selection management is unsuitable for maintaining *Acer* spp. and *Ulmus glabra*, as found by Brüllhardt (2021) and Péter-Contesse (1972), and silvicultural systems with larger gaps such as irregular shelterwood are required (Ammer and Weber 1999, El Kateb et al. 2006).

6. Conclusion

As a case study, our results represent an important stepping stone towards a general understanding of beech dominance in primary mixed old-growth beech forests. We did not find any reciprocal replacement among broadleaved species. Under the single-tree mortality that is prevailing in this forest, *Fagus sylvatica* poles are replacing conspecific hosts (self-replacement) as well as heterospecific hosts, irrespective of the neighborhood. In contrast, *Acer platanoides* and *Ulmus glabra* are not capable of self-replacement and cannot replace a heterospecific host, while this is possible, to a low degree, for *Acer pseudoplatanus* in specific locations. The proximity to dead lying trees and canopy gaps is crucial for *Acer* spp. and *Ulmus glabra* saplings for successful growth to the pole stage due to transient gap edges. A higher rate of recruitment under hosts adjacent to dead lying trees rather than under stand-alone trees suggests that the total length of gap edges may be as important as gap size or the frequency of disturbances for tree replacement. However, rapid recruitment to saplings for *Acer* spp. and *Ulmus glabra* in gaps does not warrant their dominant position in the pole class, as *Fagus sylvatica* also exhibits a high growth and recruitment rate. This implies that in the absence of frequent gap-creating disturbances, the current population of mature *Acer* spp. and *U. glabra* will be replaced by *Fagus sylvatica* on the 10 ha plot, and likely also in the Uholka-Shyrokyi Luh reserve as a whole.

CRedit authorship contribution statement

R. Petrovska: Conceptualization, Methodology. **H. Bugmann:** Methodology, Supervision. **M.L. Hobi:** Methodology, Supervision. **P. Brang:** Methodology, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

This paper is dedicated to the memory of Peter Brang (1963–2022), for all his wonderful contributions to science, his mentoring in numerous projects, and his good spirit. We acknowledge two reviewers for valuable comments and the field teams of the Swiss Federal Research Institute WSL and The Carpathian Biosphere Reserve (CBR) for gathering the forest inventory data on the 10 ha permanent plot. We thank J. Stillhard (WSL) and L. Hülsmann (U Bayreuth, Germany) for their advice regarding the statistical analyses. This research was financed through the State Secretariat for Education, Research and Innovation SERI, Switzerland.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.120939>.

References

- Ammer, C., Weber, M., 1999. Impact of silvicultural treatments on natural regeneration of a mixed mountain forest in the Bavarian Alps. In: Olsthoorn, A.F.M., Bartelink, H. H., Gardiner, J.J., Pretzsch, H., Hekhuis, H.J., Franc, A. (Eds.), *Management of mixed-species forest: silviculture and economics*. IBN-DLO, Wageningen, The Netherlands, pp. 68–78. Accessed 11 February 2021.

- Beaudet, M., Messier, C., 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* 28 (7), 1007–1015. <https://doi.org/10.1139/x98-077>.
- Beaudet, M., Messier, C., Paré, D., Brisson, J., Bergeron, Y., 1999. Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisé-des-Muir old-growth forest. Québec. *Écoscience* 6 (2), 264–271. <https://doi.org/10.1080/11956860.1999.11682527>.
- Beygelzimer, A., Kakadet, S., Langford, J., Sunil, A., Mount, D., Shengqiao, L., 2019. Package “FNN”: Fast Nearest Neighbor Search Algorithms and Applications. University of Maryland and Sunil Arya and David Mount, USA, Maryland.
- Blasco-Moreno, A., Pérez-Casany, M., Puig, P., Morante, M., Castells, E., 2019. What does a zero mean? Understanding false, random and structural zeros in ecology. *Methods Ecol. Evol.* 10 (7), 949–959. <https://doi.org/10.1111/2041-210X.13185>.
- Brewer, R., Merritt, P.G.G., 1978. Wind Throw and Tree Replacement in a Climax Beech-Maple Forest. *Oikos* 30 (1), 149–152. <http://www.jstor.com/stable/3543535>.
- Brüllhardt, M., 2021. Lichtverfügbarkeit und Wachstum von Buche und Bergahorn in Dauerwäldern. Presentation 1–18. https://ethz.ch/content/dam/ethz/special-interest/usys/ites/ites-dam/MoKo/2021/18JAN_04_Martin_Bruehlhardt.pdf.
- Brüllhardt, M., Rotach, P., Bigler, C., Nötzli, M., Bugmann, H., 2020. Growth and resource allocation of juvenile European beech and sycamore maple along light availability gradients in uneven-aged forests. *For. Ecol. Manage.* 474 (February), 118314 <https://doi.org/10.1016/j.foreco.2020.118314>.
- Bürkner, P. C. (2020). Package “brms”: Bayesian Regression Models using ‘Stan.’ doi: 10.32614/rj-2018-017.
- Brüllhardt, M., Rotach, P., Forrester, D.L., Bugmann, H., 2022. Sustainable regeneration in uneven-aged mixed deciduous forests managed by selection silviculture: the role of demographic structure. *Forestry: Int. J. For. Res.* 95 (2), 201–214. <https://doi.org/10.1093/forestry/cpab041>.
- Busing, R.T., 1996. Estimation of tree replacement patterns in an Appalachian Picea-Abies forest. *J. Veg. Sci.* 7 (5), 685–694. <https://doi.org/10.2307/3236380>.
- Busing, R.T., White, P.S., 1997. Species Diversity and Small-Scale Disturbance in an Old-Growth Temperate Forest: A Consideration of Gap Partitioning Concepts. *Oikos* 78 (3), 562. <https://doi.org/10.2307/3545618>.
- Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69 (3), 786–795. <https://doi.org/10.2307/1941027>.
- Caquet, B., Montpied, P., Dreyer, E., Epron, D., Collet, C., 2010. Response to canopy opening does not act as a filter to *Fagus sylvatica* and *Acer* sp. advance regeneration in a mixed temperate forest. *Ann. For. Sci.* 67 (1), 105. <https://doi.org/10.1051/forest/2009086>.
- Collin, A., Messier, C., Kembel, S.W., Bélanger, N., 2017. Low light availability associated with American beech is the main factor for reduced sugar maple seedling survival and growth rates in a hardwood forest of Southern Quebec. *Forests* 8 (11), 413. <https://doi.org/10.3390/f8110413>.
- Commarmot, B., Bachofen, H., Bundziak, Y., Bürgli, A., Shparyk, Y., Sukhariuk, D., et al., 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): A comparative study. *Forest Snow and Landscape Research* 79 (1–2), 45–56.
- Commarmot, B., Abegg, M., Brändli, U.-B., Hobi, L. M., Korol, M., & Lanz, A. (2013). *Inventory of the Largest Primeval Beech Forest in Europe. A Swiss-Ukrainian Scientific Adventure.* (B. Commarmot, U.-B. Brändli, F. Hamor, & V. Lavnyy, Eds.). WSL, Birmensdorf; Ukrainian National Forestry University, Lviv; CBR, Rakhiv. <http://www.wsl.ch/info/mitarbeitende/commarmot/publikationsliste.DE>.
- Culver, D.C., 1981. On using Horn’s Markov succession model. *Am. Nat.* 117 (4), 572–574. <https://www.jstor.org/stable/2460468>.
- Denslow, J.S., 1995. Disturbance and Diversity in Tropical Rain Forests: The Density Effect. *Ecol. Appl.* 5 (4), 962–968. <https://www.jstor.org/stable/2269347>.
- Drobyshchev, I.V., 2001. Effect of natural disturbances on the abundance of Norway spruce (*Picea abies* (L.) Karst.) regeneration in nemoral forests of the southern boreal zone. *For. Ecol. Manage.* 140 (151–161).
- Dröbner, L., Von Lüpke, B., 2005. Canopy gaps in two virgin beech forest reserves in Slovakia. *J. For. Sci.* 51 (10), 446–457. <https://doi.org/10.17221/4578-jfs>.
- El Kateb, H., Felbermeier, B., Schmerbeck, J., Ammer, C., & Mosandl, R. (2006). *Silviculture and Management of Mixed Mountain Forests in the Bavarian Alps.* Freising, Germany. <http://dnb.ddb.de>. Accessed 11 February 2021.
- Ellenberg, H., & Leuschner, C. (2010). Zeigerwerte der Pflanzen Mitteleuropas. In *Vegetation Mitteleuropas mit den Alpen, Zusatzmaterialien* (6th ed., p. 63). Stuttgart: UTB GmbH doi: <https://www.utb-shop.de/vegetation-mittleuropas-mit-den-alpen.html>.
- Feldmann, E., Dröbner, L., Hauck, M., Kucbel, S., Pichler, V., Leuschner, C., 2018. Canopy gap dynamics and tree understory release in a virgin beech forest, Slovakian Carpathians. *For. Ecol. Manage.* 415–416 (February), 38–46. <https://doi.org/10.1016/j.foreco.2018.02.022>.
- Feldmann, E., Glatthorn, J., Ammer, C., Leuschner, C., 2020. Regeneration dynamics following the formation of understory gaps in a Slovakian beech virgin forest. *Forests* 11 (5). <https://doi.org/10.3390/f11050585>.
- Firm, D., Nagel, T.A., Diaci, J., 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. *For. Ecol. Manage.* 257 (9), 1893–1901. <https://doi.org/10.1016/j.foreco.2008.09.034>.
- Fox, J., 1977. Alternation and coexistence of tree species. *Am. Nat.* 111 (977), 69–89. <https://www.jstor.org/stable/2459979>.
- Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. The causes, consequences, and variability of tree mortality. *Bioscience* 37 (8), 550–556. <https://doi.org/10.2307/1310665>.
- Gabrysniak, K.A., Paluch, R., Gawryś, R., 2021. 30-Year Changes in Oak-Hornbeam Forest after Windthrow. *Forests* 12 (5), 600. <https://doi.org/10.3390/f12050600>.
- Gelman, A., 2006. Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Anal.* 1 (3), 515–534. <https://doi.org/10.1214/06-BA117A>.
- Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., Rubin, D.B., 2013. *Bayesian Data Analysis* (third edit.). Chapman & Hall/CRC Press, London fl. - Bayesian Data Analysis Third edition (with errors).pdf.
- Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci.* 7 (4), 457–511. <https://doi.org/10.2307/2246134>.
- Harrell, F. E. J. (2020). Package rms: Regression modeling strategies. <http://biostat.mc.vanderbilt.edu/rms>.
- Hein, S., Collet, C., Ammer, C., Goff, N.L., Skovsgaard, J.P., Savill, P., 2009. A review of growth and stand dynamics of *Acer pseudoplatanus* L. in Europe: implications for silviculture. *Forestry* 82 (4), 361–385. <https://doi.org/10.1093/forestry/cpn043>.
- Hein, S. (2003). *Zur Steuerung von Astreinigung und Dickenwachstum bei Esche (Fraxinus excelsior L.) und Bergahorn (Acer pseudoplatanus L.)*. Retrieved from <http://www.freidok.uni-freiburg.de/volltexte/9265>.
- Hobi, M.L., Ginzler, C., Commarmot, B., Bugmann, H., 2015. Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. *Ecosphere* 6 (5). <https://doi.org/10.1890/ES14-00390.1>.
- Hoffman, M.D., Gelman, A., 2014. The no-U-turn sampler: Adaptively setting path lengths in Hamiltonian Monte Carlo. *J. Mach. Learn. Res.* 15 (2008), 1593–1623.
- Horn, 1975. Markovian properties of forest succession. In: Cody, M.L., Diamond, J. (Eds.), *Ecology and evolution of communities*. Harvard University Press, Cambridge, pp. 196–211 <https://www.hup.harvard.edu/catalog.php?isbn=9780674224445>.
- Hülsmann, L., Bugmann, H., Commarmot, B., Meyer, P., Zimmermann, S., Brang, P., 2016. Does one model fit all? Patterns of beech mortality in natural forests of three European regions. *Ecol. Appl.* 26 (8), 2465–2479. <https://doi.org/10.1002/eap.1388>.
- Jaloviari, P., Sedmáková, D., Pittner, J., Danková, L.J., Kucbel, S., Sedmák, R., Saniga, M., 2020. Gap structure and regeneration in the mixed old-growth forests of national nature reserve Sitno. Slovakia. *Forests* 11 (1), 1–25. <https://doi.org/10.3390/f11010081>.
- Janík, D., Adam, D., Hort, L., Král, K., Šamonil, P., Unar, P., Vrška, T., 2014. Tree spatial patterns of *Abies alba* and *Fagus sylvatica* in the Western Carpathians over 30 years. *Eur. J. For. Res.* 133 (6), 1015–1028. <https://doi.org/10.1007/s10342-014-0819-1>.
- Janík, D., Adam, D., Hort, L., Král, K., Šamonil, P., Unar, P., Vrška, T., 2016. Breaking through beech: A three-decade rise of sycamore in old-growth European forest. *For. Ecol. Manage.* 366, 106–117. <https://doi.org/10.1016/j.foreco.2016.02.003>.
- Jentsch, A., White, P., 2019. A theory of pulse dynamics and disturbance in ecology. *Ecology* 100 (7), e02734.
- Keren, S., Motta, R., Govedar, Z., Lucic, R., Medarevic, M., Diaci, J., 2014. Comparative structural dynamics of the Janj mixed old-growth mountain forest in Bosnia and Herzegovina: Are conifers in a long-term decline? *Forests* 5, 1243–1266. <https://doi.org/10.3390/f5061243>.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5 (2), 517–532. <https://doi.org/10.2307/1942040>.
- Kolo, H., Ankerst, D., Knoke, T., 2017. Predicting natural forest regeneration: a statistical model based on inventory data. *Eur. J. For. Res.* 136 (5–6), 923–938. <https://doi.org/10.1007/s10342-017-1080-1>.
- Korpel, S., 1995. *Die Urwälder der Westkarpaten*. Gustav Fischer Verlag, Stuttgart, Jena, New York.
- Kramer, K., Brang, P., Bachofen, H., Bugmann, H., Wohlgemuth, T., 2014. Forest Ecology and Management Site factors are more important than salvage logging for tree regeneration after wind disturbance in Central European forests. *For. Ecol. Manage.* 331, 116–128. <https://doi.org/10.1016/j.foreco.2014.08.002>.
- Kruschke, K.J., 2018. Rejecting or accepting parameter values in Bayesian estimation. *Adv. Methods Pract. Psychol. Sci.* 1 (2), 270–280. <https://doi.org/10.1177/2515245918771304>.
- Kucbel, S., Jaloviari, P., Saniga, M., Vencurik, J., Klimáš, V., 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *Eur. J. For. Res.* 129 (3), 249–259. <https://doi.org/10.1007/s10342-009-0322-2>.
- Kulla, L., Roessiger, J., Bošefa, M., Kucbel, S., Murgas, V., Vencurik, J., et al., 2023. Changing patterns of natural dynamics in old-growth European beech (*Fagus sylvatica* L.) forests can inspire forest management in Central Europe. *For. Ecol. Manage.* 529 (August 2022), 120633 <https://doi.org/10.1016/j.foreco.2022.120633>.
- Kunstler, G., Curt, T., Bouchaud, M., Lepart, J., 2005. Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. *Can. J. For. Res.* 35 (7), 1657–1668. <https://doi.org/10.1139/x05-097>.
- Larson, A.J., Franklin, J.F., 2010. The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage. *Can. J. For. Res.* 40 (11), 2091–2103. <https://doi.org/10.1139/X10-149>.
- Leder, B., 2009. Ökologie & waldbauliche Behandlung des Bergahorn. Presentation. https://www.wald-und-holz.nrw.de/fileadmin/Naturschutz/Dokumente/Behandlung_Bergahorn.pdf.
- Lemoine, N.P., 2019. Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos* 128 (7), 912–928. <https://doi.org/10.1111/oik.05985>.
- Lertzman, K.P., 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology* 73 (2), 657–669.
- Lertzman, K.P., 1995. Forest dynamics, differential mortality and variable recruitment probabilities. *Journal of Vegetation* 6 (2), 191–204.
- Lygis, V., Bakys, R., Gustiene, A., Burokiene, D., Matelis, A., Vasaitis, R., 2014. Forest self-regeneration following clear-felling of dieback-affected *Fraxinus excelsior*: focus

- on ash. *Eur. J. For. Res.* 133 (3), 501–510. <https://doi.org/10.1007/s10342-014-0780-z>.
- Madsen, P., Hahn, K., 2008. Natural regeneration in a beech-dominated forest managed by close-to-nature principles - A gap cutting based experiment. *Can. J. For. Res.* 38 (7), 1716–1729. <https://doi.org/10.1139/X08-026>.
- Makowski, D., Ben-Shachar, M.S., Chen, S.H.A., Lüdecke, D., 2019. Indices of effect existence and significance in the Bayesian framework. *Front. Psychol.* 10 <https://doi.org/10.3389/fpsyg.2019.02767>.
- Marshall, P., Camp, A.E., 2013. Disturbances in deciduous temperate forest ecosystems of the northern hemisphere : Their effects on both recent and future forest development. *Biodivers. Conserv.* 22, 1863–1893. <https://doi.org/10.1007/s10531-013-0525-1>.
- McElreath, R., Koster, J., 2014. Using multilevel models to estimate variation in foraging returns: effects of failure rate, harvest size, age, and individual heterogeneity. *Hum. Nat.* 25 (1), 100–120. <https://doi.org/10.1007/s12110-014-9193-4>.
- McNeish, D., 2016. On using Bayesian methods to address small sample problems. *Struct. Equ. Model. Multidiscip. J.* 23 (5), 750–773. <https://doi.org/10.1080/10705511.2016.1186549>.
- Mosandl, R., El Kateb, H., 1988. Die Verjüngung gemischter Bergwälder - Praktische Konsequenzen aus 10jähriger Untersuchungsarbeit. *Forstwissenschaftliches Centralblatt* 107, 2–13.
- Nagel, T.A., Diaci, J., 2006. Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. *Can. J. For. Res.* 36 (3), 629–638. <https://doi.org/10.1139/x05-263>.
- Nagel, T.A., Firm, D., Rozman, A., 2021. Intermediate disturbances are a key driver of long-term tree demography across old-growth temperate forests. *Ecol. Evol.* 11 (23), 16862–16873. <https://doi.org/10.1002/ece3.8320>.
- Nagel, T.A., Svoboda, M., Rugani, T., Diaci, J., 2010. Gap regeneration and replacement patterns in an old-growth Fagus-Abies forest of Bosnia-Herzegovina. *Plant Ecol.* 208 (2), 307–318. <https://doi.org/10.1007/s11258-009-9707-z>.
- Peck, J.E., Commarmot, B., Hobi, L.M., Zenner, E.K., 2015. Should reference conditions be drawn from a single 10 ha plot? Assessing representativeness in a 10,000 ha old-growth European beech forest. *Restor. Ecol.*, n/a/n/a. <https://doi.org/10.1111/rec.12258>.
- Péter-Contesse, J., 1972. Schweizerische Zeitschrift für Forstwesen. *Schweizerische Zeitschrift für Forstwesen* 123 (6), 349–363. <https://doi.org/10.5169/seals-765048>.
- Petrićan, A.M., von Lüpke, B., Petrićan, I.C., 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry* 80 (4), 397–412. <https://doi.org/10.1093/forestry/cpm030>.
- Petrovska, R., Bugmann, H., Hobi, M.L., Ghosh, S., Brang, P., 2021. Survival time and mortality rate of regeneration in the deep shade of a primeval beech forest. *Eur. J. For. Res.* 3, 1–16. <https://doi.org/10.1007/s10342-021-01427-3>.
- Poulson, T.L., Platt, W.J., 1996. Replacement patterns of beech and sugar maple in Warren Woods. Michigan. *Ecology* 77 (4), 1234–1253. <https://www.jstor.org/stable/2265592>.
- Puspure, I., Laivins, M., Matisons, R., & Gaitnieks, T. (2016). Understory changes in Fraxinus excelsior stands in response to dieback in Latvia. *Proceedings of the Latvian Academy of Sciences, Section B: Natural, Exact, and Applied Sciences*, 70(3), 131–137 doi: 10.1515/prolas-2016-0021.
- Rich, R.L., Frelich, L., Reich, P.B., Bauer, M.E., 2010. Detecting wind disturbance severity and canopy heterogeneity in boreal forest by coupling high-spatial resolution satellite imagery and field data. *Remote Sens. Environ.* 114 (2), 299–308. <https://doi.org/10.1016/j.rse.2009.09.005>.
- Runkle, J.R., 1981. Gap Regeneration in Some Old-growth Forests of the Eastern United States. *Ecology* 62 (4), 1041–1051. <https://doi.org/10.2307/1937003>.
- Scherrer, D., Ascoli, D., Conedera, M., Fischer, C., Maringer, J., Moser, B., et al., 2022. Canopy Disturbances Catalyse Tree Species Shifts in Swiss Forests. *Ecosystems* 25 (1), 199–214. <https://doi.org/10.1007/s10021-021-00649-1>.
- Schmidt, O., & Roloff, A. (2014). *Acer pseudoplatanus* L. In B. Roloff, A., Weisgerber, H., Lang, U., Stimm (Ed.), *Enzyklopädie der Holzgewächse: Handbuch und Atlas der Dendrologie* (pp. 1–26). Wiley-VCH Verlag GmbH & Co. KGaA doi: 10.1002/9783527678518.
- Schulze, E.D., Bouriaud, O., Wäldchen, J., Eisenhauer, N., Walentowski, H., Seele, C., et al., 2014. Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silvicultural management in central and Southeastern Europe. *Ann. For. Res.* 57 (2), 267–288. <https://doi.org/10.15287/afr.2014.273>.
- Shorohova, E., Fedorchuk, V., Kuznetsova, M., Shvedova, O., 2008. Wind-induced successional changes in pristine boreal Picea abies forest stands: Evidence from long-term permanent plot records. *Forestry* 81 (3), 335–359. <https://doi.org/10.1093/forestry/cpn030>.
- Stillhard, J., Hobi, M.L., Hülsmann, L., Brang, P., Ginzler, C., Kabal, M., et al., 2019. Stand inventory data from the 10-ha forest research plot in Uholka: 15 yr of primeval beech forest development. *Ecology* 100 (11), 2845. <https://doi.org/10.1002/ecy.2845>.
- Stillhard, J., Hobi, M.L., Brang, P., Brändli, U.B., Korol, M., Pokynchereda, V., Abegg, M., 2022. Structural changes in a primeval beech forest at the landscape scale. *For. Ecol. Manage.* 504, 119836 <https://doi.org/10.1016/j.foreco.2021.119836>.
- Taccoen, A., Piedallu, C., Seynave, I., Perez, V., Gégout-Petit, A., Nageleisen, L.M., et al., 2019. Background mortality drivers of European tree species: Climate change matters. *Proc. R. Soc. B Biol. Sci.* 286 (1900) <https://doi.org/10.1098/rspb.2019.0386>.
- Thomas, P.A., Stone, D., La Porta, N., 2018. Biological Flora of the British Isles: Ulmus glabra. *J. Ecol.* 106 (4), 1724–1766. <https://doi.org/10.1111/1365-2745.12994>.
- Valverde, T., Silvertown, J., 1997. Canopy closure rate and forest structure. *Ecology* 78 (5), 1555–1562. [https://doi.org/10.1890/0012-9658\(1997\)078\[1555:CCRAFSJ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1555:CCRAFSJ]2.0.CO;2).
- Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* 27 (5), 1413–1432. <https://doi.org/10.1007/s11222-016-9696-4>.
- Webb, S.L., Scanga, S.E., 2001. Windstorm disturbance without patch dynamics : twelve years of change in a Minnesota forest. *Ecology* 82 (3), 893–897.
- Woods, K.D., 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos* 33 (1), 31. <https://doi.org/10.2307/3544508>.
- Woods, K.D., 1984. Patterns of tree replacement: canopy effects on understory pattern in hemlock - northern hardwood forests. *Vegetatio* 56, 87–107. <https://doi.org/10.1007/BF00033051>.
- Woods, K. D. (2000). Dynamics in a late-successional disturbance intermediate forest hardwood, 81(1), 110–126.
- Yamamoto, S., 1996. Gap regeneration of major tree species in different forest types of Japan. *Vegetatio* 127 (2), 203–213. <https://doi.org/10.1007/BF00044641>.