Is uneven-aged silviculture best for maximizing ecosystem functioning, services, biodiversity and resilience in Walloon forests?

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Abstract

When an even-aged forest stand reaches maturity, it can be renewed within a limited period to maintain the even-aged structure or gradually transformed to an uneven-aged stand. However, there is still debate as to which silvicultural

approach is more profitable, conducive to carbon storage, favourable to biodiversity or resilient. In this study, we simulated the evolution of fifteen stands representative of the Walloon forest, whose initial structure was even-aged. The stands were managed according to two contrasting silvicultural approaches (continuation of the even-aged system *vs* transformation to an uneven-aged one) and the simulations were run with the SSP3-7.0 climate projections produced by five global circulation models.
Our simulations indicate that even-aged and uneven-aged silviculture yield similar outcomes in terms of carbon storage. Financial indicators were likewise largely unaffected, except in the oak-beech mixture, where uneven-aged silviculture increased profitability through the substitution of oak by beech. This shift reduced tree species diversity in uneven-aged oak-beech stands. Tree microhabitats, except in beech stands, were more abundant under uneven-aged silviculture. While mean values of forest ecosystem functioning indicators are largely comparable between the two approaches, uneven-aged stands exhibit higher temporal stability. Uneven-aged silviculture produces stands that are more wind-resistant and avoid periods of extreme vulnerability.
Our study shows that the most appropriate silviculture may vary depending on the aspect considered. Uneven-aged silviculture has a definite advantage in terms of stability, risk management and tree microhabitats. However, maintaining even-aged patches at the landscape scale remains important to facilitate the regeneration of shade-intolerant species.

Keywords: Continuous cover forestry, Uneven-aged silviculture, Process-based modelling, Stand transformation, Economic and ecological indicators, Climate change

1 Introduction

Many beneficial effects are attributed to continuous cover forestry (CCF), such as its capacity to preserve biodiversity by providing a variety of habitats for plants and animals (Zeller et al. 2023), and to enhance ecosystem resilience (Hanewinkel et al. 2014b; Lafond et al. 2014; Hilmers et al. 2020). By avoiding large-scale clear-cutting, CCF helps protect soils from erosion, maintain water quality, and preserve soil and tree carbon stocks (Roth et al. 2023). However, from a scientific perspective, rigorously demonstrating these presumed benefits remains challenging. Conducting a robust comparison between CCF and conventional rotation forestry (CRF) is difficult because there are few (and maybe even no) long-term experiments in which both silvicultural approaches have been tested under identical site conditions and monitored over sufficiently long periods, ideally covering at least one full rotation.

A further challenge lies in the fact that CCF advocates a set of practices consistent with its guiding principles, although these practices are not exclusive to this approach and can, to some extent, be integrated into CRF. While the defining feature of CCF is the maintenance of continuous forest cover, preferably achieved through an uneven-aged stand structure, it also promotes the use of native and diverse tree species, the conservation of old trees, deadwood, and endangered flora and fauna, the minimization of operational damage, wildlife management aligned with the ecosystem

carrying capacity, and the establishment of natural forest edges (Pommerening and Murphy 2004). In this study, we focus on one specific aspect: the silvicultural system (even-aged *vs* uneven-aged), while maintaining the forest cover, since no clear-cutting is considered.

When an even-aged stand reaches maturity, the old trees can be harvested all at once (clear-cutting method) or by several regeneration fellings (shelterwood method). In these cases, the stand is renewed within a limited time frame, either by planting or by natural regeneration, and the even-aged structure of the stand is maintained. Even-aged stands can also be transformed into uneven-aged ones by progressively removing mature trees (selective harvesting), favouring thereby a continuous flow of natural regeneration (Schütz 2002; Vítková and Ní Dhubháin 2013).

Whether or not uneven-aged silviculture is more profitable than even-aged silviculture is still being debated (Peura et al. 2018; Hanewinkel and Pretzsch 2000; Hanewinkel et al. 2014a; Mason et al. 2022; Stål et al. 2024). In the even-aged system, high-quality timber is harvested towards the end of the cycle. In contrast, uneven-aged silviculture enables the regular production of high-quality trees through selective individual tree management (Pommerening and Murphy 2004; Vítková and Ní Dhubháin 2013). However, this approach makes forest management more challenging, particularly when planning and carrying out harvesting (Mason et al. 2022). In addition, the profitability of uneven-aged stands partly depends on the growing stock maintained over time, as it represents a substantial amount of financial capital tied up in the forest. According to Ekholm et al. (2023), who focused on spruce-dominated forests, the even-aged rotation system provides a higher long-term yield.

Nolet et al. (2018) compared even- and uneven-aged silviculture globally and found no clear advantage of either approach for maintaining ecological diversity and processes. To continue exploring this topic, Zeller et al. (2023) examined links between forest structural attributes and species richness, as forest structure reflects both silviculture and natural dynamics. They emphasized the role of large canopy gaps, which benefit many species through increased light availability (Pawson et al. 2006; Wallendorf et al. 2007; Bogdziewicz and Zwolak 2014), and very old successional stages with microhabitat-bearing trees and abundant deadwood favouring fungi (Hilmers et al. 2018). Because even-aged systems create larger gaps whereas uneven-aged stands better retain old trees, overall ecological trends remain difficult to infer, particularly at large spatial or temporal scales.

Wind stability represents an additional dimension to consider when comparing uneven-aged *vs* even-aged silvicultural systems (Hanewinkel et al. 2014b; Mohr et al. 2024). The growing conditions in uneven-aged stands allow for a more gradual acclimatisation to wind exposure (Schelhaas 2008). In contrast, wind resistance is ensured collectively in an even-aged stand and may be compromised when neighbouring stands are harvested or when high-intensity cutting is suddenly applied in dense, mature stands. In contrast, heavy thinning carried out early in young stands can strengthen stand stability.

Carbon (C) storage in living biomass, litter, deadwood, and harvested wood products may be influenced by the silvicultural system. Assessing which system favours carbon storage requires comparing average standing C stocks over a full rotation

and accounting for harvested wood products. Studies comparing carbon balances and stocks under even-aged and uneven-aged silviculture remain inconclusive, with some reporting higher values under uneven-aged system (Seidl et al. 2007; Díaz-Yáñez et al. 2020), others finding no significant differences (Lundmark et al. 2016), or even less favourable outcomes (Nilsen and Strand 2013).

In this study, we want to tackle the following questions:

(i) What impact does the silvicultural approach (even-aged *vs* uneven-aged) have on ecosystem functioning?
(ii) Is it more profitable to manage a stand using an uneven-aged silviculture than an even-aged one?
(iii) Which of the two approaches is more conducive to wind resistance, biodiversity and carbon sequestration?

Ideally, long-term research experiments should be carried out to compare the two silvicultural approaches on the same sites for a duration equivalent to the whole rotation in the even-aged system. To our knowledge, such silvicultural trials do not currently exist, or have not yet been conducted for long enough. Long-term trials were established to monitor the transformation from even-aged plantations to irregular forests (*e.g.*, Glentress Trial Area in Scotland) but without considering any control treatment (even-aged silviculture) and with problems in the record keeping (Kerr et al. 2010).

An alternative approach is to use modelling to answer these research questions since it allows comparing stands in exactly the same ecological conditions for a long period and at a limited cost. This solution was retained by several authors to test the effect of various transformation methods and timings of initiation on productivity and profitability (Hanewinkel and Pretzsch 2000; Hanewinkel et al. 2014a; Reventlow et al. 2021; Vítková et al. 2021) as well as on carbon sequestration, stability and biodiversity (Hilmers et al. 2020).

Our aim is to simulate the evolution of fifteen stands spanning the most frequent stand composition and structure met in Southern Belgium, according to two silvicultural approaches (continuation of the even-aged system *vs* transformation to an uneven-aged one) and to compare their performances according to economic and ecological indicators. We focused on the most abundant tree species in Wallonia (Alderweireld et al. 2015) and initialized the simulations with existing even-aged stands.

We compared the two contrasted silvicultural approaches (*i.e.*, even-aged *vs* uneven-aged) under near future climate change conditions. Stand renewal was based on natural regeneration in both cases. For the even-aged approach, the shelterwood method was applied to obtain a massive regeneration within a limited period of time while the selective harvesting was used for the uneven-aged approach. No plantation was therefore achieved and the forest cover was maintained during the whole simulation in both cases.

Transforming an even-aged forest to an uneven-aged one creates a stand with a much more complex structure. From a modelling point of view, it requires a model

with a detailed spatial representation and great flexibility in the application of silvicultural operations (*e.g.*, cuttings). In addition, a process-based approach is necessary to account for the changing climate. We have therefore used a spatially explicit, individual- and process-based model (HETEROFOR) to perform the simulations (Jonard et al. 2020). Given the major role of regeneration to obtain and maintain uneven-aged structures, correct modelling of this process is essential to successfully simulate the impacts of the silvicultural approach on ecosystem functioning and services. HETEROFOR simulates regeneration dynamics based on a spatially explicit and process-based module. This represents a step forward compared to previous modelling studies focused on the transformation from even-aged to uneven-aged silvicultural system, which were based on more empirical approaches (Hanewinkel 2001; Hilmers et al. 2020; Vítková et al. 2021; Reventlow et al. 2021).

2 Materials and methods

2.1 Site description

The simulations were initialized using fifteen even-aged forest stands representative of Walloon forests. These included broadleaved stands predominantly dominated by sessile (*Quercus petraea*) or pedunculate oak (*Quercus robur*) and European beech (*Fagus sylvatica*), as well as coniferous stands primarily composed of Norway spruce (*Picea abies*), along with Douglas fir (*Pseudotsuga menziesii*), Scots pine (*Pinus sylvestris*), and European larch (*Larix decidua*). These stands were selected based on their development stage in order to start the simulations with mature forests to be regenerated within the next 30 to 50 years, namely approaching the target harvesting dimensions specified for the corresponding species (see Section 2.3.2) while still allowing time for shelterwood regeneration as well as for transformation to uneven-aged stands. The initial stand characteristics are presented in Table 1.

Most of the stands were selected among long-term monitoring sites from various international networks (Long-Term Ecosystem Research Network sites, ICP Forests level II plots) or regional experimental sites for studying mixture effects (Jonard et al. 2007) or transformation to an uneven-aged structure (Ligot et al. 2020). The climate conditions at these sites are representative of those found in Wallonia, with mean annual temperatures (MAT) ranging from 8.4 °C to 10.5 °C and mean annual precipitation (MAP) varying between 779 mm and 1 329 mm. All these sites were selected because they are well-documented and cover an appreciable gradient of site conditions and stand types (in terms of species composition, developmental stage). Detailed site characteristics are provided in Table 1.

2.2 HETEROFOR model

For the simulations, we used the HETEROFOR model, which is a spatially explicit, individual- and process-based model. This model is particularly well-suited for assessing the effects of climate change on structurally complex forest stands.

In this study, we present a brief overview of the model functioning since it has been described in detail in Jonard et al. (2020) and de Wergifosse et al. (2020a).

Table 1 Main characteristics of the stands used to initialize the simulations

	Site	Species	Tree density (N ha^{-1})	Basal area (m^2 ha^{-1})	Mean DBH ± std (cm)	Hdom (m)	Soil texture[1]	MAP (mm)	MAT (°C)
Oak	Chimay	*Quercus petraea*	68	14.2	50.5 ± 11.2	20.5	Clay loam	911	9.3
	(1.1 ha)	*Carpinus betulus*	648	5.4	9.7 ± 3.4	15.8			
		Total	*717*	*19.7*	*13.5 ± 12.8*	*19.4*			
	Stoumont	*Quercus petraea*	194	21.6	35.8 ± 12.5	21.4	Silt loam	1 124	8.6
	- Oak	*Fagus sylvatica*	56	3.2	23.8 ± 11.2	14.9			
	(1.2 ha)	*Betula pendula*	44	1.6	20.7 ± 5.3	14.9			
		Total	*302*	*26.5*	*31.2 ± 13.2*	*21.1*			
Beech	Bruxelles	*Fagus sylvatica*	77	36.9	77.4 ± 10.8	39.1	Silt loam	829	10.3
	(1.0 ha)								
	Eupen	*Fagus sylvatica*	253	20.0	28.3 ± 13.4	25.9	Clay loam	970	7.4
	(1.0 ha)								
	Virton	*Fagus sylvatica*	297	14.5	22.6 ± 10.1	23.9	Clay	1 070	9.4
	(1.4 ha)	*Fraxinus excelsior*	28	2.5	29.1 ± 14.7	21.3			
		Acer pseudoplatanus	11	1.2	27.2 ± 17.8	18.4			
		Total	*372*	*20.3*	*23.5 ± 11.4*	*24.0*			
Oak & Beech	Baileux	*Fagus sylvatica*	262	19.2	26.1 ± 15.3	28.1	Silty	953	9.3
	(1.7 ha)	*Quercus petraea*	113	15.6	41.0 ± 7.4	27.2	clay loam		
		Total	*382*	*34.8*	*30.2 ± 15.2*	*28.5*			
	Wellin	*Fagus sylvatica*	329	16.5	20.5 ± 14.6	25.3	Loam	1 061	8.8
	- OakBeech	*Quercus petraea*	42	8.8	49.6 ± 12.6	24.6			
	(1.2 ha)	*Total*	*371*	*25.3*	*23.5 ± 16.9*	*25.2*			
	Lauzelle	*Fagus sylvatica*	36	8.7	46.9 ± 34.9	23.4	Silt loam	779	10.5
	(1.4 ha)	*Quercus petraea*	20	6.8	65.3 ± 18.0	31.6			
		Acer pseudoplatanus	181	6.4	16.8 ± 12.7	24.4			
		Total	*260*	*23.4*	*24.4 ± 23.5*	*29.9*			
Spruce &| Douglas	Gedinne	*Picea abies*	217	31.4	42.4 ± 5.7	31.9	Loam	1 329	8.0
	(1.4 ha)								
	Honsfeld	*Picea abies*	761	25.3	20.1 ± 4.2	18.0	Silt loam	964	7.4
	(1.0 ha)	*Total*	*764*	*25.3*	*20.1 ± 4.2*	*18.0*			
	La Roche	*Picea abies*	607	33.8	26.2 ± 4.7	22.6	Silt loam	1 045	8.8
	(1.4 ha)	*Pseudotsuga menziesii*	34	3.7	36.1 ± 5.4	24.8			
		Total	*641*	*37.5*	*26.7 ± 5.2*	*23.5*			
	Blanche Virée	*Pseudotsuga menziesii*	549	38.5	29.2 ± 5.9	30.7	Loam	1 061	8.8
	(1.4 ha)	*Total*	*552*	*38.5*	*29.1 ± 6.0*	*30.7*			
	Stoumont	*Pseudotsuga menziesii*	128	27.9	52.2 ± 11.4	34.3	Loam	1 124	8.6
	- Conifers	*Picea abies*	141	14.0	35.4 ± 6.6	28.0			
	(1.2 ha)	*Total*	*275*	*42.3*	*41.4 ± 12.3*	*34.2*			
Pine | Larch	Wellin - Larch	*Larix decidua*	278	30.4	36.9 ± 5.7	25.4	Loam	1 061	8.8
	(1.0 ha)								
	Wellin - Pine	*Pinus sylvestris*	195	31.4	44.6 ± 8.2	21.1	Loam	1 061	8.8
	(1.1 ha)	*Betula pendula*	48	1.3	17.6 ± 5.0	14.8			
		Total	*258*	*33.0*	*37.7 ± 14.5*	*21.1*			

[1]USDA soil textural classification

Species with a basal area < 1 m^2 ha^{-1} are not individually shown but are included in the total

DBH: trunk diameter at breast height; Hdom: dominant height, defined as the average height of the 100 trees per hectare with the largest trunk diameter

Mean annual precipitation (MAP) and mean annual temperature (MAT) represent averages over the period 1980-2015, determined from ERA5 reanalysis dataset (Hersbach et al. 2020)

HETEROFOR has been developed within the CAPSIS platform (Dufour-Kowalski et al. 2012) and uses some of its librairies to describe specific processes.

2.2.1 Growth of adult trees

The model simulates growth at an annual time step and, for each year, starts by determining the main phenological stages of deciduous species (such as budburst, leaf yellowing, and leaf falling) based on meteorological data. Subsequently, the model calculates the radiation intercepted by individual trees and transmitted to the understorey based on the SAMSARALIGHT library, using a ray-tracing method (Courbaud et al. 2003; André et al. 2021).

Then, a water balance routine partitions rainfall into throughfall, stemflow and interception (André et al. 2011), calculates tree transpiration and evaporation from foliage, bark and soil using the Penman-Monteith equation (Monteith 1965), estimates root water uptake (Couvreur et al. 2012) and describes soil water movements based on the Darcy law. The model calculates the hourly gross primary production (GPP, measured in kgC tree^{-1} h^{-1}) for each tree based on the intercepted radiation and the soil water potential using the biochemical photosynthesis model from the CASTANEA library (Dufrêne et al. 2005). Next, the net primary production (NPP, in kgC tree^{-1} h^{-1}) is empirically derived from GPP using the Carbon Use Efficiency (CUE) approach. CUE is variable and depends on factors such as tree size, shape, competition for light, and mean annual temperature (MAT). The NPP is first allocated to foliage and fine roots (diameter $\leq$ 2mm), ensuring a functional balance, and then distributed to structural components using allometric equations. Dimensional growth is deduced from the biomass allocated to the aboveground structural components.

2.2.2 Regeneration development

In HETEROFOR, the regeneration phase begins with small seedlings (height $\leq$ 0.5 m) and lasts until saplings reach the recruitment height defined by the user (*e.g.*, 12 m). During this phase, the number of individuals per unit area is often too large to allow a description of growth at the individual level. This would lead to disproportionately long calculation times and would be of little interest. The regeneration development is therefore described using cohorts. A regeneration cohort is a group of seedlings/saplings of the same tree species and age. To account for the spatial heterogeneity of the regeneration, a matrix approach is used based on the cells defined for the radiation transfer (Courbaud et al. 2003; André et al. 2021). The simulated scene in HETEROFOR (*i.e.*, the stand) is divided into cells according to a systematic grid. Each regeneration cohort is associated with a cell whose size can be defined by the user (*e.g.*, 10 $\times$ 10 m). Several cohorts can be associated with the same cell.

Regeneration cohorts are generated automatically from the seed bank or specified by the user through the inventory file or the plantation intervener. The cohorts are characterized based on the tree species, the age, the number, the mean collar diameter and the mean height of the individuals (seedlings or saplings) that compose it. The model calculates the cohort cover and LAI based on these characteristics. From the radiation transmitted to each cell, a radiation budget is performed using the Beer Lambert law and provides the solar radiation received and absorbed by each cohort,

which allows estimating the mean height increment by accounting for the shade tolerance of each species (Niinemets and Valladares 2006) and the net primary production of the cohort, respectively. Based on the dimensional growth, the model calculates the mean net primary production at the individual level. The ratio between the net primary production calculated at the cohort and the individual level is the number of individuals surviving to the next time step and accounts for the self-thinning process. Once the mean height reaches a threshold value, the cohort is converted into trees in the model. These trees are randomly placed within the cohort cell and their heights are drawn from a normal distribution with a mean equal to the cohort mean height. The crown base height, the height of largest crown extension and the collar diameter are derived from the tree height using allometric relationships. The diameter at breast height is obtained based on the collar diameter and is used to determine the crown radii.

2.2.3 Tree mortality

Tree mortality can be the result of different processes. First, when a tree does not have enough carbon to support its growth, the leaf biomass is reduced inducing a defoliation that will ultimately lead to the death of the tree when the defoliation reaches 90% (de Wergifosse et al. 2020a; Jonard et al. 2020). Several factors may explain this carbon starvation: i) competition for light, when carbon assimilation becomes insufficient to maintain functional organs (i.e. corresponding to self-thinning); ii) water stress, which reduces carbon uptake in case of prolonged drought as soil drought drives stomatal closure; and iii) senescence, as carbon use efficiency tends to decrease with age.

HETEROFOR is also able to consider windstorm damage with a dedicated module based on the hybrid wind risk model ForestGALES-TMC (Hale et al. 2015). This module compares the wind speed at the top of the tree to the critical wind speed leading to overturning or stem breakage, and the subsequent impact on seedlings and neighbouring trees (see Guignabert et al. (2024) for a detailed description).

Finally, mortality may also result from tree harvesting, which can be performed using different thinning tools available in CAPSIS.

2.2.4 Model parametrization and initialization

HETEROFOR requires a significant number of parameters, the majority of which are species specific. Values for almost all parameters were either retrieved from the literature (*e.g.*, specific leaf area, leaf turnover, drought sensitivity, wood density) or were fitted using available data when dealing with empirical relationships (*e.g.*, biomass functions, crown dimension functions). In addition, two important functions require to run the model to be calibrated: the height growth function, and the carbon use efficiency. The calibration procedure is described in detail in de Wergifosse et al. (2022) and the values of the species-specific parameters are given in the supplementary material of the same paper and in Guignabert et al. (2024). Some other parameters are generic for all species or by species type (*i.e.*, broadleaved *vs* coniferous) and were presented in the supplementary material of Guignabert et al. (2023).

The performances of the model in terms of radial and height growth were evaluated for European tree species using data from long-term forest monitoring networks in

Europe (level II plots of ICP Forests) (Jonard et al. 2020; de Wergifosse et al. 2022; Guignabert et al. 2024). A detailed assessment of phenology processes (budburst, leaf development, yellowing and fall) and water balance dynamics (throughfall, extractable water, individual transpiration, deep drainage) was also carried out by de Wergifosse et al. (2020a) using highly monitored stands of beech and oak (both pure and mixed) in Wallonia.

For the initialization, the model requires various data describing: (i) soil horizons, (ii) stand and (iii) meteorological conditions at an hourly or daily time step. The data necessary for the model initialization are described in detail in de Wergifosse et al. (2022). For each stand, we used the data collected by the research program to which the plot belongs.

2.3 Simulation experiment

2.3.1 Simulation setup

The simulations were run with SSP3-7.0 climate projections produced by five global circulation models (GCMs) and bias-adjusted with the univariate ISIMIP3BASD method (Lange 2019; Lange et al. 2021) using the W5E5 dataset (Lange et al. 2021). Given that climate change is already underway and expected to continue, we based our analysis on a scenario that incorporates projected future conditions rather than historical climate. We excluded SSP5-8.5, as it is increasingly regarded as less plausible in light of current emission trends. Instead, we selected SSP3-7.0 as a plausible high-end forcing scenario. This pathway reflects limited mitigation efforts and relatively strong warming (increase of 3.6 °C by 2100), making it well suited to evaluating the robustness of management strategies under substantial climatic stress (Frieler et al. 2025). Our aim was not to represent a central or most likely trajectory, but rather to assess how silvicultural strategies perform under challenging yet plausible future conditions.

To account for uncertainty in climate projections, we used an ensemble of five GCMs under SSP3-7.0, thereby capturing a range of possible temperature and precipitation trajectories. This ensemble approach avoids reliance on any single climate projection, whose specific biases or variability could unduly influence the results. Instead, it allows us to sample a set of plausible future climates and to assess the consistency of management effects across contrasting climate realizations. The five GCMs (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0 andUKESM1-0-LL) were selected based on the provided climate variables, the model performance during the historical period, and their representation of key processes, their structural independence and their climate sensitivity (Lange et al. 2021). To avoid the uncertainties associated with the CO_2 fertilization effect, the simulations were conducted using a fixed atmospheric CO_2 concentration (430 ppm).

All simulations were initiated in 2015, though the duration of each varied according to the type of stand. Simulations, with a duration of 250 years, were conducted for oak-dominated stands, given the relatively slow growth rate of this tree species. For stands dominated by beech, a simulation duration of 200 years was selected, while for coniferous stands, given their rapid growth, the duration was reduced to 100 years. Given that the available climate projections extend only to 2100, the climate data

for all subsequent years was randomly selected from within the final 30 years of the projection series.

2.3.2 Silvicultural routes

For each stand, two simulations were carried out considering contrasting silvicultural routes with the aims of either maintaining an even-aged stand or evolving towards an uneven-aged structure, so as to compare both silvicultural approaches. As presented in Table 2, the modalities of the silvicultural routes were defined according to regional silvicultural guidelines. The cuttings were achieved using interveners (i.e. algorithms that defines the trees to be cut according to fixed rules) developed specifically for HETEROFOR, but partly inspired by those developed by Ligot et al. (2023) and already available in CAPSIS.

For the simulations aiming at perpetuating the even-aged structure, the existing stand was grown until it reached the harvesting dimension (*i.e.*, a tree average trunk diameter at breast height close to the harvesting DBH value mentioned in Table 2). Shelterwood harvesting was then carried out uniformly over the stand area in several cuts performed every six years. The number of shelterwood cuts was fixed according to shade tolerance of the main tree species. For more shade tolerant species, the shelterwood harvesting was made over a longer period of time and therefore with more numerous but less intensive cuttings (Table 2). As the 'regeneration from seed' option was selected, regeneration cohorts appeared automatically. The stand was then conducted following regional silvicultural guidelines or yield tables from the literature (Table 2). In HETEROFOR, the silvicultural guidelines are formulated as follows: for successive ranges of dominant height, the target stand basal area after thinning, the maximum thinning intensity as well as the thinning type (from above, mixed or from below) are specified. The thinning cuts were carried out from below with periodicities of 12 and 6 years for broadleaved and coniferous species, respectively.

Furthermore, in oak stands, the hornbeam coppice was cut every 12 years, leaving around 1 m^2 ha^{-1} standing basal area after harvest for this accompanying species.

The stand transformation to uneven-aged systems was achieved by felling the trees that had reached the harvesting dimension at each cutting cycle and by completing these silvicultural operations with mixed thinnings where necessary, limiting the harvest intensity to maximum 20-25% of the basal area to prevent stand destabilization. The cutting cycle was 6 years for coniferous stands and 12 years for broadleaved ones. For a given species, the target basal area post-cutting was set by selecting the upper end of the range recommended by Sanchez (2013).

2.3.3 Simulation analysis

The analysis of the simulation results (*e.g.*, comparison of the two silvicultural scenarios for different stand types) were conducted on the basis of indicators of forest ecosystem functioning, provision of ecosystem services, wind resistance and biodiversity.

Forest ecosystem functioning was assessed using three key indicators, gross primary production (GPP), net primary production (NPP), and evapotranspiration

Table 2 Main specifications of the silvicultural routes used for the simulations

Species	Even-aged silviculture		Uneven-aged silviculture		Harvesting DBH (cm)	Clearings	
	Cutting modalities	Progressive cuts	Cutting modalities[3,4]	Target basal area (m^2 ha^{-1})		Height range (m)	Target density (N ha^{-1})
Oak[1]	Thinnings from below every 12 years following the yield table of Sardin (2008)	3	Harvest of trees with DBH > 79.6 cm and mixed thinnings, every 12 years	16	79.6	5 - 8	2 000
Hornbeam	Coppice harvest every 12 years		Coppice harvest every 12 years	1			
Beech[2]	Thinnings from below every 12 years following the yield table of Vannière (1984)	4	Harvest of trees with DBH > 70.0 cm and mixed thinnings, every 12 years	18	70.0	7 - 10	4 000
Spruce	Thinnings from below every 6 years following the yield table of Perin et al. (2016)	4	Harvest of trees with DBH > 47.7 cm and mixed thinnings, every 6 years	33	47.7	7 - 10	2 000
Douglas fir	Thinnings from below every 6 years following the yield table of Perin et al. (2016)	3	Harvest of trees with DBH > 66.8 cm and mixed thinnings, every 6 years	34	66.8	7 - 10	2 000
Larch	Thinnings from below every 6 years following the yield table of Pauwels (2003)	2	Harvest of trees with DBH > 66.8 cm and mixed thinnings, every 6 years	27	66.8	5 - 10	1 000
Pine	Thinnings from below every 6 years following the yield table of Vannière (1984)	2	Harvest of trees with DBH > 57.3 cm and mixed thinnings, every 6 years	27	57.3	5 - 8	1 500

[1] Regeneration clearings were carried out to promote oak seedlings: i) for even-aged silviculture, every year during progressive cuts; ii) for uneven-aged silviculture competing species were reduced to a cover of 10% every 3 years when oaks were 0-3 m in height, and to a density of 500/ha every 6 years when oaks were 3-6 m in height

[2] Additional thinnings were carried out at mid-rotation in the presence of fast-growing species (maple, in Louvain-la-Neuve).

[3] Values after thinning, following Sanchez (2013).

[4] Harvest trunk diameter at breast height (DBH) for secondary species are 63.7 cm for maple, 57.3 cm for ash and 44.6 for birch.

(ETP), which were evaluated based on their annual mean values and temporal stability over the simulation period. These variables represent major carbon and water fluxes and provide insights into forest productivity and overall vitality, while evapotranspiration also constitutes an important climate service due to its cooling effect at local and regional scales. Stability, defined as the inverse of the coefficient of variation ($stability = \mu/\sigma$), characterizes the temporal dynamics of the forest and its ability to maintain consistent level of functioning through time. Higher stability can therefore be attributed to an increase in the mean value of the indicator and/or a reduction in its standard deviation. Other ecosystem services were also considered, including wood production and carbon storage, both of which can be partly characterized by the average annual volume increment ($\overline{I_{vol}}$, m^3 ha^{-1} $year^{-1}$) over the whole simulation period, calculated using:

$$\overline{I_{vol}} = \frac{Vol_{harv} + (Vol_{end} - Vol_{init})}{n} \tag{1}$$

where Vol_{harv}, Vol_{init} and Vol_{end} (m^3 ha^{-1}) are the cumulated commercial volume harvested during the simulation and the commercial volumes of the initial and the final stands, respectively, and n is the number of years covered by the simulation. For broadleaved trees, the commercial volume is defined as the stem volume between the ground and the height at which the stem diameter is the half of that at breast height (Delevoy volume), while it corresponds to the stem volume up to the 7 cm diameter height level for coniferous.

The average annual profit (AAP, € ha^{-1} $year^{-1}$) was used as a financial indicator for wood production, determined as:

$$AAP = \frac{\sum_{i=0}^{n}(I_i - E_i) + (SV_{end} - SV_{init})}{n} \tag{2}$$

where I_i and E_i (€ ha^{-1}) are, respectively, the incomes (*i.e.*, sales of harvested trees, hunting rents) and the expenses (*i.e.*, costs of silvicultural operations, property and personal income taxes) for year i, and SV_{init} and SV_{end} are the stumpage values (€ ha^{-1}) of the initial and the final stands, respectively.

Another financial indicator considered is the net present value (NPV) of the stand, including land value (LV), expressed in euros per ha (€ ha^{-1}). It is calculated as (Vítková et al. 2021):

$$NPV = \sum_{i=0}^{n} \frac{I_i - E_i}{(1+r)^i} + \frac{LV + SV_{end}}{(1+r)^n} \tag{3}$$

where r is the discount rate, set at 1.25% for broadleaved stands and 2.5% for coniferous stands, reflecting the average internal rate of return on the respective forest properties in Wallonia.

These financial indicators were computed using ECONOMICS2 (Ligot 2021), but with some adaptations to obtain the indicators specific to HETEROFOR. These calculations require several information, including price lists for timber and forestry operations as well as forest land value. The economical data used for this work are presented in Tables S1 and S2.

Regarding carbon storage, two indicators were considered: the carbon budget and the mean carbon stock. The carbon budget represents the sum of the change in living biomass over the simulation period, the carbon stored in forest products still in use at the end of the simulation, and the cumulative carbon emissions and substitution effects that occurred during the simulation. The mean carbon stock corresponds to the average amount of carbon stored throughout the simulation in deadwood, litter, soil, living biomass, and forest product compartments. We assumed that the carbon content of the mineral soil remained constant over the entire simulation period and was not influenced by the silvicultural treatment. The implications and limitations of this assumption are discussed in the Discussion section.

The carbon stored in forest products, as well as the associated carbon emissions and substitution effects, were estimated by coupling HETEROFOR with CAT, a carbon accounting software designed to assess the carbon balance of managed forests. CAT follows the guidelines of the Intergovernmental Panel on Climate Change (IPCC) for national greenhouse gas inventories in the Land Use, Land-Use Change and Forestry (LULUCF) and Waste sectors (Pichancourt et al. 2018). In addition to the dynamics of aboveground and belowground living biomass and dead organic matter compartments also simulated by HETEROFOR, CAT accounts for the harvested wood product (HWP) carbon pool, both in use and deposited in landfill sites. Using a user-customizable flux configuration scheme that describes the carbon life cycle of wood products, including transformation, recycling, and disposal stages, CAT also provides estimates of:

(i) material and energy substitution, corresponding to greenhouse gas emissions avoided when HWPs replace alternative products;
(ii) fossil fuel carbon emissions associated with the HWP life cycle;
(iii) changes in degradable and non-degradable HWPs at landfill sites;
(iv) emissions from HWP degradation (CH_4) and wood combustion (CH_4, CO, VOCs).

For this project, a flux configuration scheme developed for the Walloon wood processing sector, based on the works of Wohlfrom (2022) and Charles (2023), was applied.

The dynamics of aboveground and belowground living biomass, as well as dead organic matter compartments, were simulated by both HETEROFOR and CAT. However, only the outputs provided by HETEROFOR were used to calculate the indicators.

The simulations were also compared in terms of wind resistance, assessed from storms occurring at 10-year intervals with a wind gust intensity of 40 m s^{-1}. Using the wind damage module described in Guignabert et al. (2024), the model computes the proportion of undamaged trees, expressed in terms of basal area, at each 10-year interval, and then calculates the minimum and the mean values over the entire simulation period.

Finally, based on the work of Courbaud et al. (2017), Courbaud et al. (2022) and Larrieu et al. (2022) whose outcomes were first implemented in the SAMSARA2

model of CAPSIS and then reused in HETEROFOR, the level of biodiversity was expressed as a score integrating the size, the frequency, the degree of rarity and the replacement rate of the tree-related microhabitats (TreMs) appearing on each tree during the simulations (Larrieu and Amberger Unpublished). The higher the score, the higher is the ecological interest of a tree with regard to its TreMs.

For different stand types (broadleaved *vs* coniferous) and species compositions, the effect of the silvicultural approach (even-aged *vs* uneven-aged) on each indicator was evaluated using Wilcoxon tests, as all the indicators did not meet the assumption of normality.

To partition the variability of each indicator into the contributions of site, silvicultural scenario, global circulation model, and residual variability, the following mixed-effects linear model was fitted for each indicator with the *lmer* function from the *lme4* package of the R software (R Core Team 2022):

$$Indicator_{species} = [Silv + GCM]_{fixed} + [Site]_{random} + \epsilon \quad (4)$$

where the silvicultural scenario ($Silv$) and the global circulation model (GCM) were set as fixed effects and the site ($Site$) was included as a random effect. The interaction terms among these factors were not considered as they did not appear to be significant or were only slightly significant.

3 Results

3.1 General overview of the stand dynamics simulations

For all the simulations performed according to an even-aged approach, the temporal change in basal area followed a similar pattern (Figure 1). After an initial period of stability, which corresponded to the time required for the stand to reach the harvesting dimension, a series of shelterwood cuts gradually harvested all the mature trees in the stand and led to a sharp decline in basal area. With the growth of the regeneration cohorts, basal area began to rise again to recover a level equivalent to that observed before the shelterwood cuts. Except for the periods of shelterwood cuts and regeneration, the basal area followed a jagged pattern (repetition of the sequence: gradual increase due to tree growth followed by a drop of the same magnitude due to cutting). Simulations according to an uneven-aged approach show a much higher stability in basal area. In most cases, the basal area remained stable in the long-term while following a jagged evolution in a shorter term. The oak stands in Chimay and Stoumont exhibited greater fluctuations in basal area compared to the other stands. This pattern likely reflects the episodic nature of oak regeneration, which occurred in waves despite efforts to promote continuous regeneration.

When comparing tree species, one can note that the basal area was maintained at a much higher level in coniferous stands and somewhat higher under beech than under oak. Except during the regeneration phase, basal areas were larger in even-aged stands when compared with uneven-aged ones. This was particularly true for broadleaved species (Figure 1).

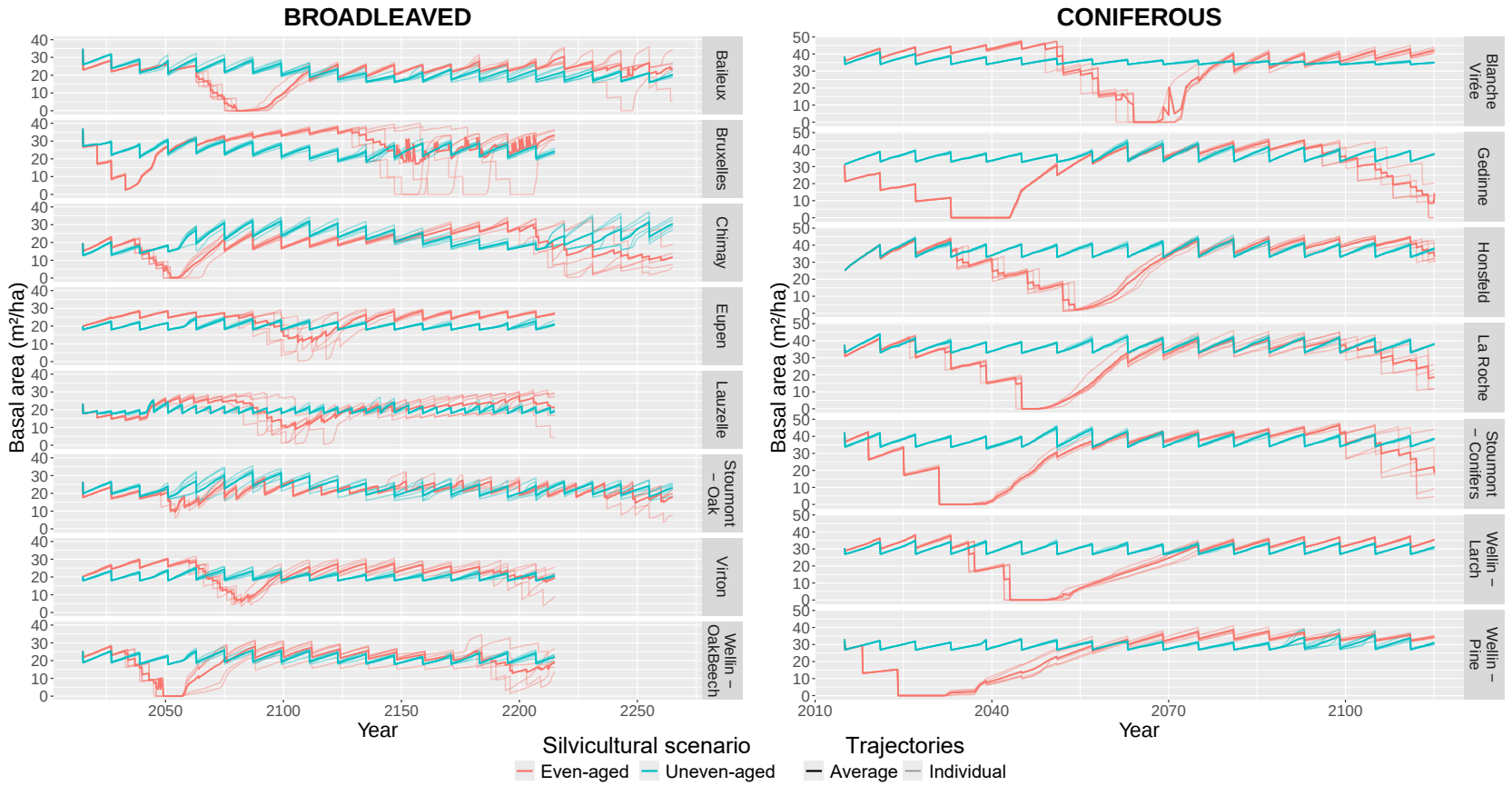

Fig. 1 Temporal variation of the stand basal area for each silvicultural scenario and for each site. Seedlings are not considered. For each silvicultural scenario, the semi-transparent lines show the simulations from the five GCMs, while the opaque line represents the mean of these five simulations.

3.2 Impact of the silvicultural scenario on ecosystem functioning, profitability, wind resistance, biodiversity and carbon storage indicators

The mixed-effects linear models used to partition indicator variability (Equation 4, Table 3) explained around 90% of the variance for GPP, NPP, evapotranspiration, profit, net present value, volume increment, wind resistance, and Simpson index (Figure 2). For stability indicators, minimum wind resistance, TreMs score and carbon budget, the proportion of explained variance was lower (57-84%), whereas it was 96% for carbon storage. The site effect, encompassing the stand type, the soil and the climate influences, accounted for more than 85% of the explained variance for all indicators except NPP stability, evapotranspiration stability and minimum wind resistance for which it was around 75%. For GPP, NPP, evapotranspiration, evapotranspiration stability, profit, net present value, volume increment, carbon budget and, to a lesser extent, carbon storage, the second most influential factor was the GCM, which accounted for 1-18% of the explained variance. However, for GPP stability, NPP stability, wind resistance, minimum wind resistance, and the Simpson index, the silvicultural scenario was more important, accounting for 2-25% of the explained variance.

The silvicultural scenario had only a minor influence on the mean indicators of forest ecosystem functioning (GPP, NPP, and ETP). In broadleaved stands, NPP under the uneven-aged scenario was 6% lower than under the even-aged scenario, whereas in coniferous stands, ETP was 6% higher in the uneven-aged scenario compared to the even-aged one (Figure 2). The reduction in NPP in broadleaved stands conducted with an uneven-aged silviculture was limited to beech stands, whereas the increase in ETP was observed only in spruce and/or Douglas fir stands (Figure S1). Although average indicators show little effect, differences emerge in terms of stability, which was generally higher under the uneven-aged scenario, particularly for coniferous stands (Figure 2).

Overall, no effect of the silvicultural scenario was observed on financial indicators related to wood production (profit, net present value). Nonetheless, these indicators were consistently higher in coniferous stands compared with broadleaved stands (Figure 2). At the level of individual stand types, the uneven-aged scenario showed greater profitability in mixed oak and beech stands (volume increment increased by 15%, profit by 17% and net present value by 24%) (Figure S1).

Wind resistance was higher under the uneven-aged silviculture than under the even-aged silviculture. In broadleaved stands, wind resistance (already higher than in coniferous stands) increased from 0.81 to 0.86 when shifting to an uneven-aged structure. In coniferous stands, it increased more modestly, from 0.47 to 0.51 (Figure 2). When considering individual stand types, wind resistance was enhanced in oak stands, oak and beech mixtures, as well as in pure or mixed spruce and Douglas fir stands (Figure S1). We also examined the minimum wind resistance over the simulation period, which corresponds to the state of highest vulnerability to wind damage. For this variable, differences are much more pronounced, with minimum wind resistance in uneven-aged broadleaved stands reaching 0.54, compared with 0.29 under the

even-aged scenario. For coniferous stands, the contrast is even stronger, with values of 0.21 and 0.02 for the uneven-aged and even-aged scenarios, respectively Figure 2).

Regarding biodiversity indicators, the Simpson index revealed that tree species diversity was 40% lower in uneven-aged broadleaved stands (particularly in oak and beech mixtures). In contrast, tree microhabitats (TreMs score) were 12% more abundant in uneven-aged coniferous stands (particularly in pure or mixed stands composed of spruce and/or Douglas fir). Both indicators remained consistently lower in coniferous compared with broadleaved stands. The apparent lack of silvicultural effect on the TreMs score in broadleaved stands masked contrasting species-specific responses: in beech stands, the TreMs score was lower under the uneven-aged scenario, while in oak stands, it was higher (Figure S1).

The carbon budget was positive in all cases, being approximately fourfold higher in coniferous compared with broadleaved stands, mainly due to the spruce and/or Douglas stands. The carbon budget was more favourable under coniferous stands due to an increase in living biomass (while a decrease was observed for broadleaved stands), a higher storage in harvested wood products and a larger substitution effect (Figure 3). In broadleaved stands, the carbon budget was 18% greater under the uneven-aged scenario than under the even-aged one. This effect was observed in oak stands and in oak and beech mixtures, but not in pure beech stands. It partly resulted from an increased living biomass in oak stands and a higher substitution effect in oak and beech mixtures managed under an uneven-aged silvicultural scenario (Figure S2). The silvicultural scenario had no overall effect on carbon storage, except in pure pine or larch stands, which showed higher storage under the uneven-aged scenario. This effect was mainly due to storage in living biomass and harvested forest products (Figure S2).

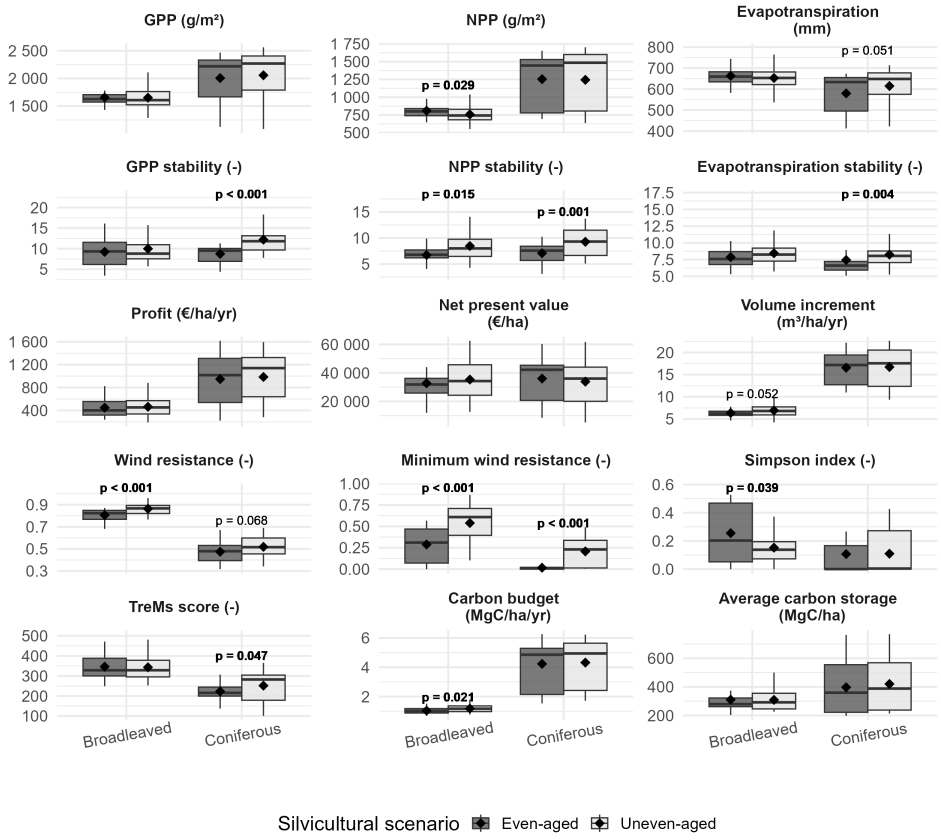

Fig. 2 Assessment of the silvicultural scenario effect on various indicators for broadleaved and coniferous stands. In each boxplot, the inner horizontal line represents the median value, the diamond symbol represents the mean value, the lower and upper ends of the box correspond to the 25^{th} ($Q1$) and the 75^{th} ($Q3$) percentiles, respectively, which delimit the interquartile range (IQR), and the extremities of the whiskers correspond to the minimum and maximum values determined as $Q1 - 1.5 \times IQR$ and as $Q3 + 1.5 \times IQR$, respectively. Significant differences among silvicultural scenarios for a given species type (P-value ≤ 0.05) are indicated in bold, while potential but non-significant trends ($0.05 <$ P-value ≤ 0.1) are shown in regular font.

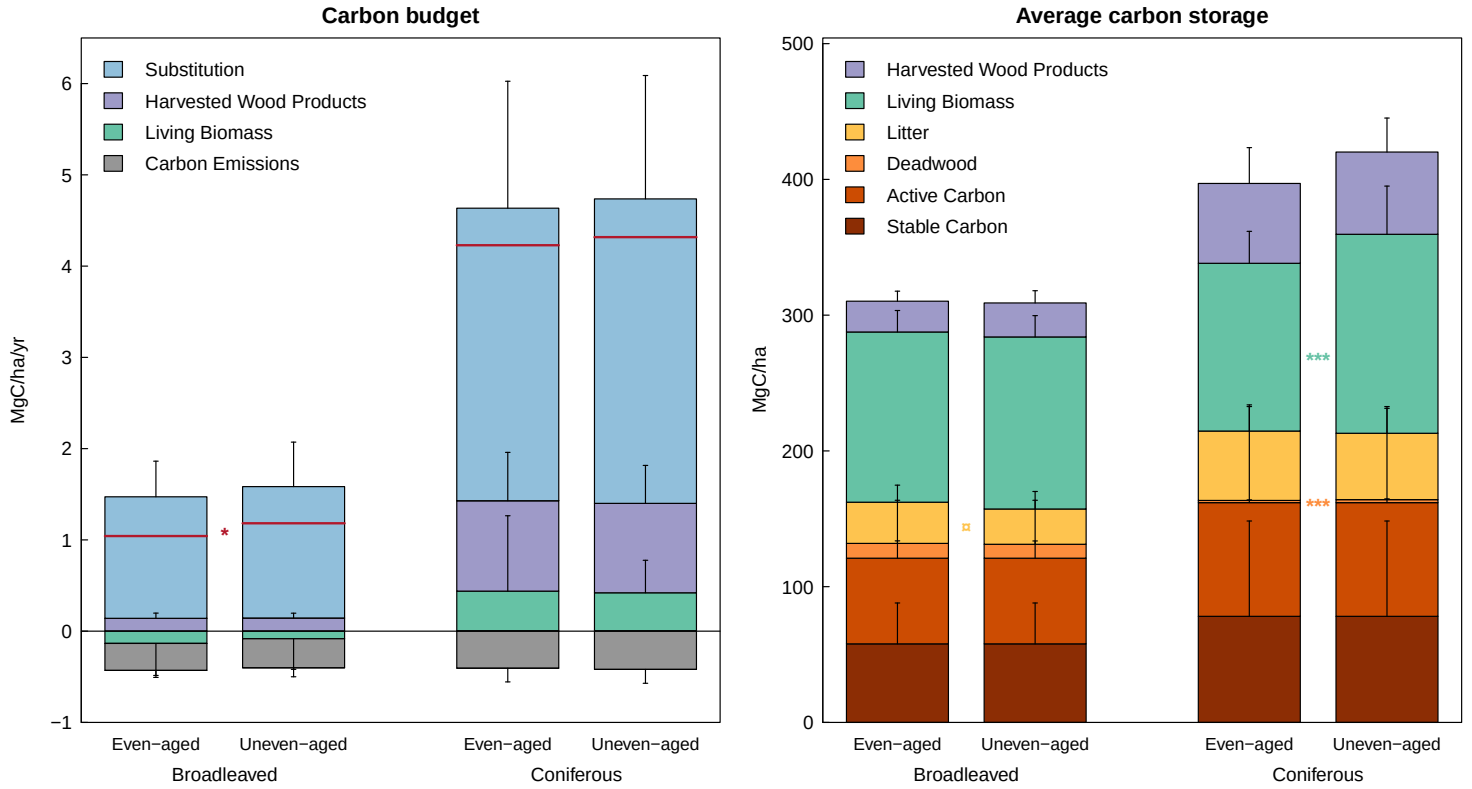

Fig. 3 Effect of the silvicultural scenario on carbon budget and average carbon storage components for broadleaved and coniferous stands. The error bars represent the standard deviations for each component. The red horizontal lines show the net carbon budget level. The stars indicate significant differences. Active carbon and stable carbon are two components of mineral soil carbon. Active carbon is the fraction that is readily decomposed by macro-organisms, while stable carbon is the fraction that is more resistant to decomposition.

4 Discussion

4.1 Ecosystem functioning and carbon storage

Our simulation results indicate that uneven-aged silviculture had only limited effects on the mean values of the ecosystem functioning indicators considered, with two notable exceptions: (i) a slight reduction in NPP in uneven-aged beech stands and (ii) higher ETP rates in uneven-aged spruce and/or Douglas-fir stands. In contrast, more pronounced differences emerged in their temporal dynamics, with stands managed under uneven-aged silviculture exhibiting higher stability, particularly in coniferous stands.

For beech, the lower NPP in uneven-aged stands appears to be primarily driven by a difference in growing stock rather than intrinsic effects of the silvicultural scenario itself. Basal area dynamics differed substantially between the two silvicultural approaches; overall, the uneven-aged silviculture resulted in lower mean basal area in beech stands (22 *vs* 24 m^2 ha^{-1}), which in turn reduced stand LAI by about 22% and consequently diminished light interception and NPP. This lower mean basal area is consistent with the fact that uneven-aged silviculture guidelines for temperate broadleaved forests are typically built around low upper limits of growing stock to secure continuous regeneration, maintain adequate light in the understorey, and ensure sufficient recruitment across cohorts (Brüllhardt et al. 2022). Our findings suggest that basal area thresholds in uneven-aged stands can have an effect as important as the silvicultural system itself. In line with our results, Kellomäki et al. (2019) used a forest ecosystem model to compare even-aged and uneven-aged silviculture in boreal Norway spruce and showed that mean annual carbon uptake and growth were very similar under both approaches. Consistent with our findings, they reported that differences in productivity (*e.g.*, GPP and NPP) were limited once stand basal area was considered.

In spruce and Douglas-fir, the uneven-aged scenario resulted in a higher mean basal area (37 *vs* 31 m^2 ha^{-1}), diverging from the response observed in beech; however, this increase did not yield differences in LAI. In this case, the higher structural heterogeneity may have contributed to the observed increased in evapotranspiration. Uneven-aged structure tends to favour evapotranspiration because it enhances light penetration to lower canopy strata and increases understory evaporation (Beaudet et al. 2004; Kassuelke et al. 2022). These processes intensify stand-level water loss even when total LAI remains unchanged. For spruce and Douglas-fir, the uneven-aged silviculture guidelines recommend a target basal area that is much higher than for beech (Table 2) and closer to the levels suggested for even-aged stands. The high basal area thresholds for uneven-aged spruce and Douglas-fir stands may seem surprising given the lower shade tolerance of these species (compared to beech). The reason for this is the fact that conifers have thinner crown and needs less space to develop than broadleaved trees such as beech (Schütz 1997). Additionally, it is important to remember that, unlike conifers, beech seedlings lose their ability to grow upright if they remain in the shade for too long (Schütz 2002). This raises the broader question of how basal area thresholds might be optimized to balance regeneration requirements

Table 3 Contributions of the site, silvicultural scenario and climate model effects to the variance of the indicators derived from the simulations

Effects[1]	**GPP**			**NPP**			**Evapotranspiration**		
	% explained variance	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**
Site	92.8	85.8	<0.001	92.0	79.2	<0.001	91.7	81.1	<0.001
Silvi	0.3	0.2	0.032	0.8	0.7	0.006	0.6	0.5	0.011
GCM	6.9	6.4	<0.001	7.2	6.2	<0.001	7.7	6.9	<0.001
Residuals		7.6			13.9			11.5	
	GPP stability			**NPP stability**			**Evapotranspiration stability**		
	% explained variance	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**
Site	85.4	57.6	<0.001	75.9	43.3	<0.001	74.6	51.8	<0.001
Silvi	10.3	7.0	<0.001	19.5	11.1	<0.001	7.0	4.9	<0.001
GCM	4.3	2.9	0.013	4.6	2.6	0.068	18.4	12.8	<0.001
Residuals		32.5			43.0			30.5	
	Profit			**Net present value**			**Volume increment**		
	% explained variance	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**
Site	93.4	86.0	<0.001	94.7	84.8	<0.001	88.5	75.6	<0.001
Silvi	0.3	0.3	0.020				0.7	0.6	0.015
GCM	6.3	5.7	<0.001	5.3	4.7	<0.001	10.8	9.3	<0.001
Residuals		8.0			10.5			14.5	
	Wind resistance			**Minimum wind resistance**			**Simpson index**		
	% explained variance	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**
Site	95.2	82.0	<0.001	75.1	62.3	<0.001	97.9	85.8	<0.001
Silvi	4.8	4.1	<0.001	24.9	20.6	<0.001	2.1	1.9	<0.001
GCM									
Residuals		13.9			17.1			12.3	
	TreMs score			**Carbon budget**			**Average carbon storage**		
	% explained variance	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**	**% explained variance**	**% total variance**	**P-value**
Site	100.0	70.6	<0.001	90.9	75.8	<0.001	98.7	95.1	<0.001
Silvi				1.5	1.3	0.001	0.3	0.2	0.002
GCM				7.6	6.4	<0.001	1.0	1.0	<0.001
Residuals		29.4			16.5			3.7	

[1]Site: encompassing the influence of the stand type (Oak, Beech, Oak & Beech, Spruce &| Douglas, Pine | Larch), the soil and the climate, Silvi: silvicultural scenario (Even-aged, Uneven-aged), GCM: General circulation model

with stand productivity and carbon storage. It would be interesting to make further simulation tests (as well as *in situ* trials) to refine these standards.

Even if there is limited effect of the silvicultural scenario on evapotranspiration, the uneven-aged stands may be more resistant and resilient to drought since the young trees are protected from the stressing conditions of the atmosphere by their underlying position within the canopy (Bennett et al. 2015). They can also take over the dominant ones in case of mortality induced by water stress.

The silvicultural scenario, and consequently stand structure, appears to have only limited effects on the overall carbon budget. In all cases, the substitution effect accounts for the majority of the average carbon budget, highlighting the importance of product use strategy for long-term carbon mitigation independent of management options (Lundmark et al. 2016). Compared to the silvicultural scenario, the forest type (broadleaved *vs* coniferous) exerts a much stronger influence. Coniferous stands showed an increase in living biomass and volume of harvested wood products remaining in use, whereas most broadleaved stands exhibited a reduction in living biomass, apart from uneven-aged oak stands. This exception resulted in a higher carbon budget for oak managed under uneven-aged silviculture.

There is also no effect of the silvicultural scenario on total carbon stocks, which are likely to be more sensitive to stocking density and, consequently, to the standards applied in classical and continuous-cover forestry in Wallonia. This is consistent with previous studies reporting no or minimal differences between silvicultural systems, with generally slightly higher C stock in soils under uneven-aged systems and slightly higher C stock in biomass under even-aged systems (Nilsen and Strand 2013; Lundmark et al. 2016; Peura et al. 2018). However, other studies have shown a positive effect of uneven-aged silviculture on total C storage (Seidl et al. 2007; Díaz-Yáñez et al. 2020), suggesting that no clear or consistent trend emerges across studies. Change in soil carbon storage was not considered in this study. It may however be higher in the uneven-aged stands, as demonstrated in French forests by Jonard et al. (2017), since they are subject to less disturbance due to less intensive harvesting, especially for the final cuttings (Mayer et al. 2020).

4.2 Economic assessment

The silvicultural scenario also had no significant impact on financial indicators, except for the oak-beech mixture. In this case, the observed increase in profitability associated with the uneven-aged silviculture appears to be driven primarily by a tree species substitution effect. Even-aged silviculture has been shown to be more effective at maintaining the original species composition, largely due to the abundant regeneration of oak achieved using the shelterwood method (Pohl et al. 2025). In contrast, uneven-aged silviculture has tended to result in a gradual replacement of oak by beech over time. This tree species substitution resulted in higher stand productivity since beech grows faster, which translated into improved economic performance. In mixed-species stands, shifts in species composition can have a more pronounced impact on financial outcomes than the silvicultural approaches themselves.

One may question whether using a different discount rate would have changed our conclusions. We tested several discount rates (1.25%, 2%, 3%, 5%) and found that it did not affect the relative results.

We assumed that the regeneration and harvesting costs did not differ between the two silvicultural approaches since natural regeneration was applied in both cases. A more in-depth cost analysis would enable us to verify this hypothesis, but this type of information is not readily available.

Previous studies comparing even-aged and uneven-aged silviculture based on financial indicators have also relied on modelling approaches, as long-term trials are scarce and often insufficiently documented (Kerr et al. 2010). Most of this work focuses on the transformation of pure even-aged Norway spruce stands into uneven-aged pure or mixed stands (Hanewinkel 2001; Hilmers et al. 2020; Vítková et al. 2021; Reventlow et al. 2021). These studies report both negative and positive impacts of such transformations, which can be interpreted as the absence of a clear overall effect, consistent with the pattern observed in our study. Hanewinkel (2001) obtained a lower net present value (NPV) with the transformation to an uneven-aged stand and this effect was more pronounced with a lower discount rate (1% *vs* 3%). As Hanewinkel (2001), Reventlow et al. (2021) obtained a lower expectation value for the transformation compared to the classical even-aged silviculture, except for some scenarios with an older initial stand (60 years old instead of 30 years old) and a higher discount rate (3%). They also found that several trajectories can produce a balanced uneven-aged stand but with large differences in the time needed to obtain it. They were in favour of the creation of small gaps to achieve a quick transformation with a high profitability due to early incomes. With younger initial stands, Vítková et al. (2021) obtained higher land expectation values for the transformation scenarios than for the even-aged scenarios while the transformation of older stands was found to be less economically viable. This contrasts with the results of Reventlow et al. (2021) but can partly be explained by the fact that the age of the old stands (60 years old) in Reventlow et al. (2021) corresponds to that of the young stands (52 years old) in Vítková et al. (2021). This importance of initial conditions was also reported by Kellomäki et al. (2019) who showed that economic assessment of uneven-aged silviculture is more favourable when conducted from already mature stands rather than since the time of planting. The uncertainties on the financial impact of transformations are thus still large, and it is not clear how these depend on the species, the initial conditions and the region studied.

4.3 Biodiversity and wind resistance

Biodiversity was assessed based on two indicators: the abundance of tree-related microhabitats (TreMs score) and the tree species diversity (Simpson index). The substitution of beech for oak in the uneven-aged oak and beech stands reduced tree species diversity. Except for the beech stands, the TreMs score was generally higher for the uneven-aged silviculture than for the even-aged one. At the stand scale, the TreMs score was obtained by summing the individual score of each living tree bearing microhabitats. The individual score depends on the size/abundance of the microhabitats on the tree and on the type of microhabitats (Larrieu and Amberger Unpublished). This

individual score tended to increase with age, as older and larger trees are more likely to contain large and rare microhabitats (Courbaud et al. 2017, 2022). However, this is not only the age and species of the trees that matter at the stand level, but also the density of the trees. The higher score for the uneven-aged stands compared to the even-aged ones can be explained by the combination of a high tree density and the presence of old large trees (Peura et al. 2018). An important advantage of uneven-aged stands is also that many habitat types are kept over time, which is particularly beneficial for species with limited dispersal (Larrieu et al. 2022). In even-aged systems, species associated with large trees and deadwood may be temporarily lost and can be slow (or fail) to recolonize. In the case of beech, the massive recruitment that occurred under the even-aged scenario explains why the TreMs score was higher for this system. Biodiversity is a highly complex concept that is very difficult to summarize in one or more indices (Larrieu et al. 2022), and other dimensions of biodiversity besides tree diversity and TreMs could have also been considered, such as the spatial heterogeneity (in its horizontal and vertical dimensions) and the understorey vegetation.

One of the most evident effects of the silvicultural approach concerns wind resistance. Stands managed under uneven-aged silviculture exhibit greater resistance to wind damage, whereas mature even-aged stands approaching the end of the rotation are much more vulnerable to storms. While uneven-aged stands may experience low levels of wind damage at any time, even-aged stands can suffer complete destruction at advanced stages of development, especially in coniferous stands. The higher wind resistance of uneven-aged stands is likely due to the growth conditions in which the trees develop. In uneven-aged stands, recruited trees develop under lower stand densities, resulting in larger crowns and greater individual acclimation to wind-induced mechanical stresses. Moreover, the number of large trees likely to be blown over by the wind is more limited in such stands (Schelhaas 2008). Furthermore, the presence of understorey trees reduces the loading on adult trees by dissipating part of the gust energy (Gardiner et al. 2005). In contrast, wind stability in even-aged stands is primarily expressed at the collective stand level, particularly under conditions of high stand density. These even-aged stands are particularly vulnerable when they reach an advanced stage of development and when wind-sensitive species are present. The transition phase, during which dense, mature even-aged stands are progressively opened to initiate transformation into an uneven-aged structure, constitutes also a period of heightened vulnerability to wind damage (Vítková and Ní Dhubháin 2013).

4.4 Importance of initial stand conditions

The mixed-effects linear models used to decompose the total variance of the different indicators showed that initial site conditions play a predominant role in explaining the variability (43 to 95%), particularly through stand characteristics such as species composition, developmental stage, and density. In contrast, the effect of the silvicultural system, which can be partly attributed to differences in density or species composition dynamics associated with the uneven-aged silviculture, explained only a limited share of the variability (0.2 to 20.6%) as well as the GCMs (1 to 13%).

Site conditions not only exert a decisive influence on the various indicators, but also play a key role in guiding the choice of the most appropriate silvicultural approach.

Indeed, the suitability of a given approach strongly depends on the local context. When natural regeneration is abundant, composed of desirable species, and of good quality, uneven-aged silviculture is particularly appropriate. This approach offers greater resilience, notably through higher resistance to disturbances and a better capacity for recovery, as younger cohorts can replace dominant trees in the event of damage. However, natural regeneration can be difficult to achieve due to irregular fructification (*e.g.*, in oak), the shade intolerance of certain tree species, and pressure from ungulate browsing (Candaele et al. 2023). Moreover, transformation toward uneven-aged stands is not recommended when the risk of windthrow is high, as is the case in old, dense Norway spruce stands (Reventlow 2020). Conversely, even-aged silviculture may be more suitable for the regeneration of shade-intolerant species or with irregular fructification. For instance, in mixed oak and beech forests in Wallonia, maintaining oak is often advantageous, as it is better adapted to projected future climatic conditions, supports higher associated biodiversity, and yields higher-quality timber.

To strengthen resilience and maximise ecosystem services at the landscape scale, attention must be paid not only to structural heterogeneity within individual stands, but also to the diversity of stand structures across the landscape, including both even-aged and uneven-aged stands (Vítková and Ní Dhubháin 2013).

However, it must be acknowledged that even-aged silviculture is often associated with conventional forestry practices that can be highly disruptive for the soil, including clear-cutting, the use of heavy equipment such as harvester-processors and skidders, and various forms of soil preparation. These impacts, however, are not inevitable: harvesting can be conducted using more soil-conserving techniques, and regeneration can take place under an existing canopy through the shelterwood method. Similarly, managing a stand as uneven-aged does not, by itself, prevent soil compaction by machinery unless specific protective measures are implemented.

4.5 Uncertainties and limitations of the approach

Uncertainty in future climate was partially captured using projections from five GCMs, but it accounted for only a limited share of the overall variability (∼5%). However, our approach relies on a single emissions pathway (SSP3-7.0), which does not encompass the full range of uncertainty associated with future climate projections. In this study, we deliberately limited the level of complexity to focus primarily on the silvicultural scenarios. However, HETEROFOR has already been used to investigate the effects of climate change on forest ecosystem functioning (de Wergifosse et al. 2020b, 2022), and will continue to serve this purpose in future work. We are currently developing a tree hydraulics module that accounts for hydraulic failure and its consequences for tree vitality. Compared with the model version used in this study, this development will enable the representation of drought-induced mortality not only through carbon starvation, but also through hydraulic failure or a combination of both mechanisms. Once validated against historical data, this module will be used to generate future projections of forest dynamics. Exploring scenarios with contrasting radiative forcing, together with activating the tree hydraulics module, would provide valuable complementary insights. However, the influence of natural mortality on forest dynamics is likely to remain limited in a managed forest context as long as mortality

rates stay well below harvesting intensity. As growth rates would likely differ among scenarios, harvesting intensity would be adjusted accordingly under our approach. If the capacity of forest management to absorb dead or declining trees is exceeded, however, forest dynamics could be substantially altered, requiring alternative silvicultural approaches. Assessing such strategies falls beyond the scope of the present study, but has been examined in Guignabert et al. (2024).

5 Conclusion

Our simulation study indicates that, under comparable conditions and using natural regeneration, even-aged and uneven-aged silviculture yield similar outcomes in terms of profitability and carbon storage. While mean values of forest ecosystem functioning indicators are largely comparable between the two approaches, uneven-aged stands exhibit higher temporal stability, particularly in coniferous forests. In terms of biodiversity, species richness tends to be higher under even-aged silviculture, whereas tree microhabitats are more abundant in uneven-aged stands. Moreover, uneven-aged silviculture produces stands that are more wind-resistant and avoid periods of extreme vulnerability, unlike mature even-aged coniferous stands. All scenarios were based on regional guidelines; however, repeating the simulations while varying target basal areas could provide further insights, as growing stock appears to influence some indicators more strongly than stand structure.

References

Alderweireld M, Burnay F, Pitchugin M, Lecomte H (2015) Inventaire Forestier Wallon. Résultats 1994 - 2012. SPW, DGO3, DNF, Direction des Ressources forestières, Jambes. ISBN: 978-2-8056-0171-2, URL https://ediwall.wallonie.be/inventaire-forestier-wallon-resultats-1994-2012-2015-104319

André F, de Wergifosse L, de Coligny F, Beudez N, Ligot G, et al (2021) Radiative transfer modeling in structurally complex stands: towards a better understanding of parametrization. Ann For Sci 78(4):92. https://doi.org/10.1007/s13595-021-01106-8

André F, Jonard M, Jonard F, Ponette Q (2011) Spatial and temporal patterns of throughfall volume in a deciduous mixed-species stand. J Hydrol 400(1-2):244–254. https://doi.org/10.1016/j.jhydrol.2011.01.037

Beaudet M, Messier C, Leduc A (2004) Understorey light profiles in temperate deciduous forests: Recovery process following selection cutting. J Ecol 92(2):328–338. https://doi.org/10.1111/j.0022-0477.2004.00869.x

Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ (2015) Larger trees suffer most during drought in forests worldwide. Nat Plants 1:15139. https://doi.org/10.1038/nplants.2015.139

Bogdziewicz M, Zwolak R (2014) Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: A meta-analysis and review. Eur J For Res 133(1):1–11. https://doi.org/10.1007/s10342-013-0726-x

Brüllhardt M, Rotach P, Forrester DI, Bugmann H (2022) Sustainable regeneration in uneven-aged mixed deciduous forests managed by selection silviculture: the role of demographic structure. Forestry 95(2):201–214. https://doi.org/10.1093/forestry/cpab041

Candaele R, Ligot G, Licoppe A, Lievens J, Fichefet V, et al (2023) Interspecific growth reductions caused by wild ungulates on tree seedlings and their implications for temperate Quercus-Fagus forests. Forests 14(7):1330. https://doi.org/10.3390/f14071330

Charles G (2023) Evaluation de l'influence de la sylviculture sur le bilan carbone de la filière forêt-bois wallonne. Master Thesis, Gembloux Agro-Bio Tech, Université de Liège, URL https://matheo.uliege.be/bitstream/2268.2/18242/5/TFE_Charles_Guillaume.pdf

Courbaud B, de Coligny F, Cordonnier T (2003) Simulating radiation distribution in a heterogeneous Norway spruce forest on a slope. Agric For Meteorol 116(1-2):1–18. https://doi.org/10.1016/S0168-1923(02)00254-X

Courbaud B, Pupin C, Letort A, Cabanettes A, Larrieu L (2017) Modelling the probability of microhabitat formation on trees using cross-sectional data. Methods Ecol Evol 8(10):1347–1359. https://doi.org/10.1111/2041-210X.12773

Courbaud B, Larrieu L, Kozak D, Kraus D, Lachat T, et al (2022) Factors influencing the rate of formation of tree-related microhabitats and implications for biodiversity conservation and forest management. J Appl Ecol 59(2):492–503. https://doi.org/10.1111/1365-2664.14068

Couvreur V, Vanderborght J, Javaux M (2012) A simple three-dimensional macroscopic root water uptake model based on the hydraulic architecture approach. Hydrol Earth Syst Sci 16(8):2957–2971. https://doi.org/10.5194/hess-16-2957-2012

Dufour-Kowalski S, Courbaud B, Dreyfus P, Meredieu C, de Coligny F (2012) Capsis: An open software framework and community for forest growth modelling. Ann For Sci 69(2):221–233. https://doi.org/10.1007/s13595-011-0140-9

Dufrêne E, Davi H, François C, le Maire G, Le Dantec V, et al (2005) Modelling carbon and water cycles in a beech forest Part I : Model description and uncertainty analysis on modelled NEE. Ecol Model 185:407–436. https://doi.org/10.1016/j.ecolmodel.2005.01.004

Díaz-Yáñez O, Pukkala T, Packalen P, Peltola H (2020) Multifunctional comparison of different management strategies in boreal forests. Forestry 93(1):84–95. https:

//doi.org/10.1093/forestry/cpz053

Ekholm A, Lundqvist L, Petter Axelsson E, Egnell G, Hjältén J, et al (2023) Long-term yield and biodiversity in stands managed with the selection system and the rotation forestry system: A qualitative review. For Ecol Manage 537:120920. https://doi.org/https://doi.org/10.1016/j.foreco.2023.120920

Frieler K, Lange S, Schewe J, Mengel M, Treu S, et al (2025) Scenario set-up and the new CMIP6-based climate-related forcings provided within the third round of the Inter-Sectoral Model Intercomparison Project (ISIMIP3b, group I and II). EGUsphere 2025:1–70. https://doi.org/10.5194/egusphere-2025-2103

Gardiner B, Marshall B, Achim A, Belcher R, Wood C (2005) The stability of different silvicultural systems: A wind-tunnel investigation. Forestry 78(5):471–484. https://doi.org/10.1093/forestry/cpi053

Guignabert A, Ponette Q, André F, Messier C, Nolet P, et al (2023) Validation of a new spatially explicit process-based model (HETEROFOR) to simulate structurally and compositionally complex forest stands in eastern North America. Geosci Model Dev 16(6):1661–1682. https://doi.org/10.5194/gmd-16-1661-2023

Guignabert A, Jonard M, Messier C, André F, de Coligny F, et al (2024) Adaptive forest management improves stand-level resilience of temperate forests under multiple stressors. Sci Total Environ 948. https://doi.org/10.1016/j.scitotenv.2024.174168

Hale SA, Gardiner B, Peace A, Nicoll B, Taylor P, et al (2015) Comparison and validation of three versions of a forest wind risk model. Environ Model Softw 68:27–41. https://doi.org/10.1016/j.envsoft.2015.01.016

Hanewinkel M (2001) Economic aspects of the transformation from even-aged pure stands of Norway spruce to uneven-aged mixed stands of Norway spruce and beech. For Ecol Manage 151:181–193. https://doi.org/10.1016/S0378-1127(00)00707-6

Hanewinkel M, Pretzsch H (2000) Modelling the conversion from even-aged to uneven-aged stands of Norway spruce (Picea abies L. Karst.) with a distance-dependent growth simulator. For Ecol Manage 134(1-3):55–70. https://doi.org/10.1016/S0378-1127(99)00245-5

Hanewinkel M, Frutig F, Lemm R (2014a) Economic performance of uneven-aged forests analysed with annuities. Forestry 87(1):49–60. https://doi.org/10.1093/forestry/cpt043

Hanewinkel M, Kuhn T, Bugmann H, Lanz A, Brang P (2014b) Vulnerability of uneven-aged forests to storm damage. Forestry 87(4):525–534. https://doi.org/10.1093/forestry/cpu008

Hersbach H, Bell B, Berrisford P, Hirahara S, Horányi A, et al (2020) The ERA5 global reanalysis. Q J R Meteorol Soc 146(730):1999–2049. https://doi.org/10.1002/qj.3803

Hilmers T, Friess N, Bässler C, Heurich M, Brandl R, et al (2018) Biodiversity along temperate forest succession. J Appl Ecol 55(6):2756–2766. https://doi.org/10.1111/1365-2664.13238

Hilmers T, Biber P, Knoke T, Pretzsch H (2020) Assessing transformation scenarios from pure Norway spruce to mixed uneven-aged forests in mountain areas. Eur J For Res 139(4):567–584. https://doi.org/10.1007/s10342-020-01270-y

Jonard M, André F, Jonard F, Mouton N, Procès P, et al (2007) Soil carbon dioxide efflux in pure and mixed stands of oak and beech. Ann For Sci 64(2):141–150. https://doi.org/10.1051/forest:2006098

Jonard M, Nicolas M, Coomes DA, Caignet I, Saenger A, et al (2017) Forest soils in France are sequestering substantial amounts of carbon. Sci Total Environ 574:616–628. https://doi.org/10.1016/j.scitotenv.2016.09.028

Jonard M, André F, de Coligny F, de Wergifosse L, Beudez N, et al (2020) HETEROFOR 1.0: a spatially explicit model for exploring the response of structurally complex forests to uncertain future conditions ? Part 1: Carbon fluxes and tree dimensional growth. Geosci Model Dev 13(3):905–935. https://doi.org/10.5194/gmd-13-905-2020

Kassuelke SR, Dymond SF, Feng X, Savage JA, Wagenbrenner JW (2022) Understory evapotranspiration rates in a coast redwood forest. Ecohydrol 15(3). https://doi.org/10.1002/eco.2404

Kellomäki S, Strandman H, Peltola H (2019) Effects of even-aged and uneven-aged management on carbon dynamics and timber yield in boreal Norway spruce stands: A forest ecosystem model approach. Forestry 92(5):635–647. https://doi.org/10.1093/forestry/cpz040

Kerr G, Morgan G, Blyth J, Stokes V (2010) Transformation from even-aged plantations to an irregular forest: The world's longest running trial area at Glentress, Scotland. Forestry 83(3):329–344. https://doi.org/10.1093/forestry/cpq015

Lafond V, Lagarrigues G, Cordonnier T, Courbaud B (2014) Uneven-aged management options to promote forest resilience for climate change adaptation: Effects of group selection and harvesting intensity. Ann For Sci 71(2):173–186. https://doi.org/10.1007/s13595-013-0291-y

Lange S (2019) Trend-preserving bias adjustment and statistical downscaling with ISIMIP3BASD (v1.0). Geosci Model Dev 12(7):3055–3070. https://doi.org/10.5194/gmd-12-3055-2019

Lange S, Menz C, Gleixner S, Cucchi M, Weedon G, et al (2021) WFDE5 over land merged with ERA5 over the ocean (W5E5 v2.0). https://doi.org/10.48364/ISIMIP.342217

Larrieu L, Amberger C (Unpublished) Ecological tree scoring system based on TreMs for marteloscopes

Larrieu L, Courbaud B, Drénou C, Goulard M, Bütler R, et al (2022) Key factors determining the presence of Tree-related Microhabitats: A synthesis of potential factors at site, stand and tree scales, with perspectives for further research. For Ecol Manage 515:120235. https://doi.org/10.1016/j.foreco.2022.120235

Ligot G (2021) Guide d'utilisation de la librairie ECONOMICS2 (Capsis4). https://orbi.uliege.be/handle/2268/263994 [last visited 28 may 2024]

Ligot G, Balandier P, Schmitz S, Claessens H (2020) Transforming even-aged coniferous stands to multi-aged stands: An opportunity to increase tree species diversity? Forestry 93(5):616–629. https://doi.org/10.1093/FORESTRY/CPAA004

Ligot G, Gheysen T, Perin J, Candaele R, de Coligny F, et al (2023) From the simulation of forest plantation dynamics to the quantification of bark-stripping damage by ungulates. Eur J For Res 142(4):899–916. https://doi.org/10.1007/s10342-023-01565-w

Lundmark T, Bergh J, Nordin A, Fahlvik N, Poudel BC (2016) Comparison of carbon balances between continuous-cover and clear-cut forestry in Sweden. Ambio 45:203–213. https://doi.org/10.1007/s13280-015-0756-3

Mason WL, Diaci J, Carvalho J, Valkonen S (2022) Continuous cover forestry in Europe: usage and the knowledge gaps and challenges to wider adoption. Forestry 95(1):1–12. https://doi.org/10.1093/forestry/cpab038

Mayer M, Prescott CE, Abaker WEA, Augusto L, Cécillon L, et al (2020) Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. For Ecol Manage 466:118127. https://doi.org/10.1016/j.foreco.2020.118127

Mohr J, Thom D, Hasenauer H, Seidl R (2024) Are uneven-aged forests in Central Europe less affected by natural disturbances than even-aged forests? For Ecol Manage 559. https://doi.org/10.1016/j.foreco.2024.121816

Monteith JL (1965) Evaporation and environment. Symp Soc Exp Biol 19:205–234

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate Northern hemisphere trees and shrubs. Ecol Monogr 76(4):521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

Nilsen P, Strand LT (2013) Carbon stores and fluxes in even- and uneven-aged Norway spruce stands. Silva Fenn 47(4). https://doi.org/10.14214/sf.1024

Nolet P, Kneeshaw D, Messier C, Béland M (2018) Comparing the effects of even- and uneven-aged silviculture on ecological diversity and processes: A review. Ecol Evol 8(2):1217–1226. https://doi.org/10.1002/ece3.3737

Pauwels D (2003) Conception d'un système d'aide à la décision pour le choix d'un scénario sylvicole. Application aux peuplements de mélèze en Région wallonne. Ph.D. Thesis, Faculté universitaire des Sciences agronomiques, Gembloux, Belgium, URL https://orbi.uliege.be/handle/2268/111193

Pawson SM, Brockerhoff EG, Norton DA, Didham RK (2006) Clear-fell harvest impacts on biodiversity: Past research and the search for harvest size thresholds. Can J For Res 36(4):1035–1046. https://doi.org/10.1139/X05-304

Perin J, Lejeune P, Hébert J, Claessens H (2016) Nouvelles normes sylvicoles pour les peuplements purs équiennes d'épicéa et de douglas. Report, Gembloux Agro-Bio Tech, Université de Liège, URL https://orbi.uliege.be/bitstream/2268/198122/1/Normes%20EP%20DO%201.2.pdf

Peura M, Burgas D, Eyvindson K, Repo A, Mönkkönen M (2018) Continuous cover forestry is a cost-efficient tool to increase multifunctionality of boreal production forests in Fennoscandia. Biol Conserv 217:104–112. https://doi.org/https://doi.org/10.1016/j.biocon.2017.10.018

Pichancourt JB, Manso R, Ningre F, Fortin M (2018) A carbon accounting tool for complex and uncertain greenhouse gas emission life cycles. Environ Model Softw 107:158–174. https://doi.org/10.1016/j.envsoft.2018.06.005

Pohl NS, Hedwall PO, Aldea J, Felton AM, Gardiner ES, et al (2025) Effects of stand structural attributes on oak recruitment in mixed temperate forests. For Ecol Manage 586:122721. https://doi.org/10.1016/j.foreco.2025.122721

Pommerening A, Murphy ST (2004) A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77(1):27–44. https://doi.org/10.1093/forestry/77.1.27

R Core Team (2022) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing

Reventlow D (2020) Transitioning to near-natural forest management: Effects on stand structure and wood production. Ph.D. Thesis, University of Copenhagen, Faculty of Science, Department of Geosciences and Natural Resource Management, Denmark, URL https://soeg.kb.dk/permalink/45KBDK_KGL/1pioq0f/alma99123768570405763

Reventlow DOJ, Nord-Larsen T, Biber P, Hilmers T, Pretzsch H (2021) Simulating conversion of even-aged Norway spruce into uneven-aged mixed forest: effects of different scenarios on production, economy and heterogeneity. Eur J For Res 140(4):1005–1027. https://doi.org/10.1007/s10342-021-01381-0

Roth EM, Karhu K, Koivula M, Helmisaari HS, Tuittila ES (2023) How do harvesting methods applied in continuous-cover forestry and rotation forest management impact soil carbon storage and degradability in boreal Scots pine forests? For Ecol Manage 544:121144. https://doi.org/10.1016/j.foreco.2023.121144

Sanchez C (2013) La sylviculture pro silva en Wallonie : Mesures et recommandations du DNF. Forêt Wallonne, URL https://www.prosilvawallonie.be/sites/default/files/documents/infoProSilva.pdf

Sardin T (2008) Chênaies continentales. Guides de sylviculture, Office national des forêts. ISBN: 978-2-84207-321-3

Schelhaas MJ (2008) The wind stability of different silvicultural systems for Douglas-fir in the Netherlands: A model-based approach. Forestry 81(3):399–414. https://doi.org/10.1093/forestry/cpn028

Schütz J (1997) Sylviculture 2 : La gestion des forêts irrégulières et mélangées. Presses Polytechniques et Universitaires Romandes, Lausanne. ISBN: 978-2-88074-349-9

Schütz J (2002) Silvicultural tools to develop irregular and diverse forest structures. Forestry 75(4):329–337. https://doi.org/10.1093/forestry/75.4.329

Seidl R, Rammer W, Jäger D, Currie WS, Lexer MJ (2007) Assessing trade-offs between carbon sequestration and timber production within a framework of multi-purpose forestry in Austria. For Ecol Manage 248(1-2):64–79. https://doi.org/10.1016/j.foreco.2007.02.035

Stål G, Nordin A, Wikberg PE, Arnesson Ceder L, Lundmark T (2024) Potential consequences of a rapid transition from rotation forestry to continous cover forestry in Sweden. Scand J For Res 39(7-8):367–376. https://doi.org/10.1080/02827581.2024.2437409

Vannière B (1984) Tables de production pour les forêts françaises. ENGREF, 2e Edition, Nancy. ISBN: 978-2-85710-016-4

Vítková L, Ní Dhubháin A (2013) Transformation to continuous cover forestry - a review. Ir For 70:119–140

Vítková L, Saladin D, Hanewinkel M (2021) Financial viability of a fully simulated transformation from even-aged to uneven-aged stand structure in forests of different ages. Forestry 94(4):479–491. https://doi.org/10.1093/forestry/cpab005

Wallendorf MJ, Porneluzi PA, Gram WK, Clawson RL, Faaborg J (2007) Bird response to clear cutting in Missouri Ozark Forests. J Wildl Manage 71(6):1899–1905. https://doi.org/10.2193/2006-386

de Wergifosse L, André F, Beudez N, de Coligny F, Goosse H, et al (2020a) HETEROFOR 1.0: a spatially explicit model for exploring the response of structurally complex forests to uncertain future conditions ? Part 2: Phenology and water cycle. Geosci Model Dev 13(3):1459–1498. https://doi.org/10.5194/gmd-13-1459-2020

de Wergifosse L, André F, Goosse H, Caluwaerts S, de Cruz L, et al (2020b) CO2 fertilization, transpiration deficit and vegetation period drive the response of mixed broadleaved forests to a changing climate in Wallonia. Ann For Sci 77(3):70. https://doi.org/10.1007/s13595-020-00966-w

de Wergifosse L, André F, Goosse H, Boczon A, Cecchini S, et al (2022) Simulating tree growth response to climate change in structurally diverse oak and beech forests. Sci Total Environ 806:150422. https://doi.org/10.1016/j.scitotenv.2021.150422

Wohlfrom P (2022) Les produits bois et leur potentiel de stockage de carbone : une solution dans l'atténuation du changement climatique ? Etude des résineux issus de la filière bois wallonne. Master Thesis, Université Libre de Bruxelles, Belgium, URL https://mem-envi.ulb.be/wp-content/uploads/2023/03/WOHLFROM-Perrine_6525867_assignsubmission_file_MFE_WOHLFROM_21-22.pdf

Zeller L, Förster A, Keye C, Meyer P, Roschak C, et al (2023) What does literature tell us about the relationship between forest structural attributes and species richness in temperate forests? - A review. Ecol Indic 153:110383. https://doi.org/10.1016/j.ecolind.2023.110383