



# Effet de la densité des peuplements et de la pression des ongulés sur la régénération dans le contexte du changement climatique

**Gauthier Ligot**

*Gembloux Agro-Bio Tech, University of Liege, Belgium*



Continuous cover  
forestry

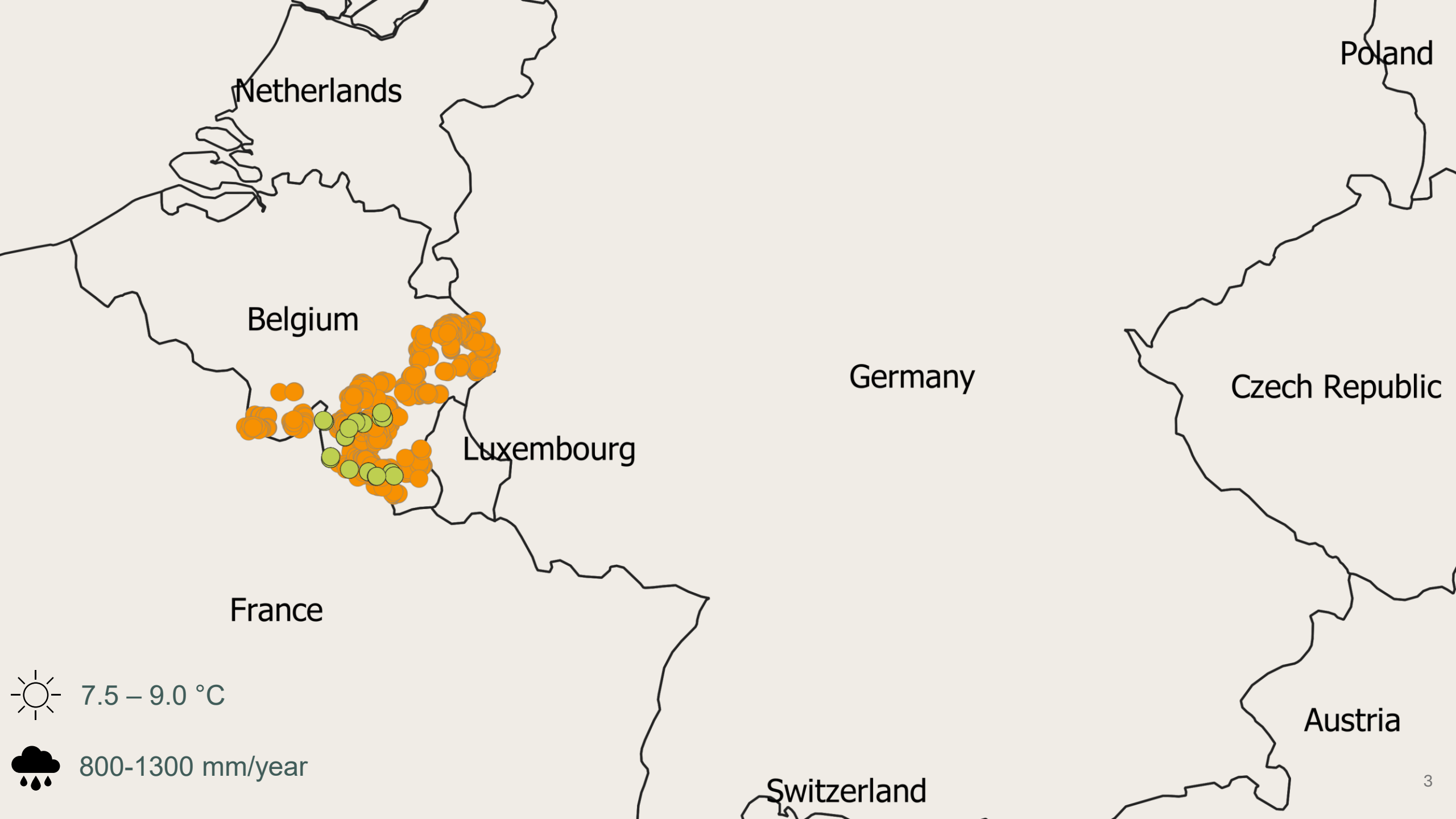
Natural regeneration

Global changes

Resilience

Diversification





Netherlands

Poland

Belgium

Germany

Czech Republic

Luxembourg

France

Austria

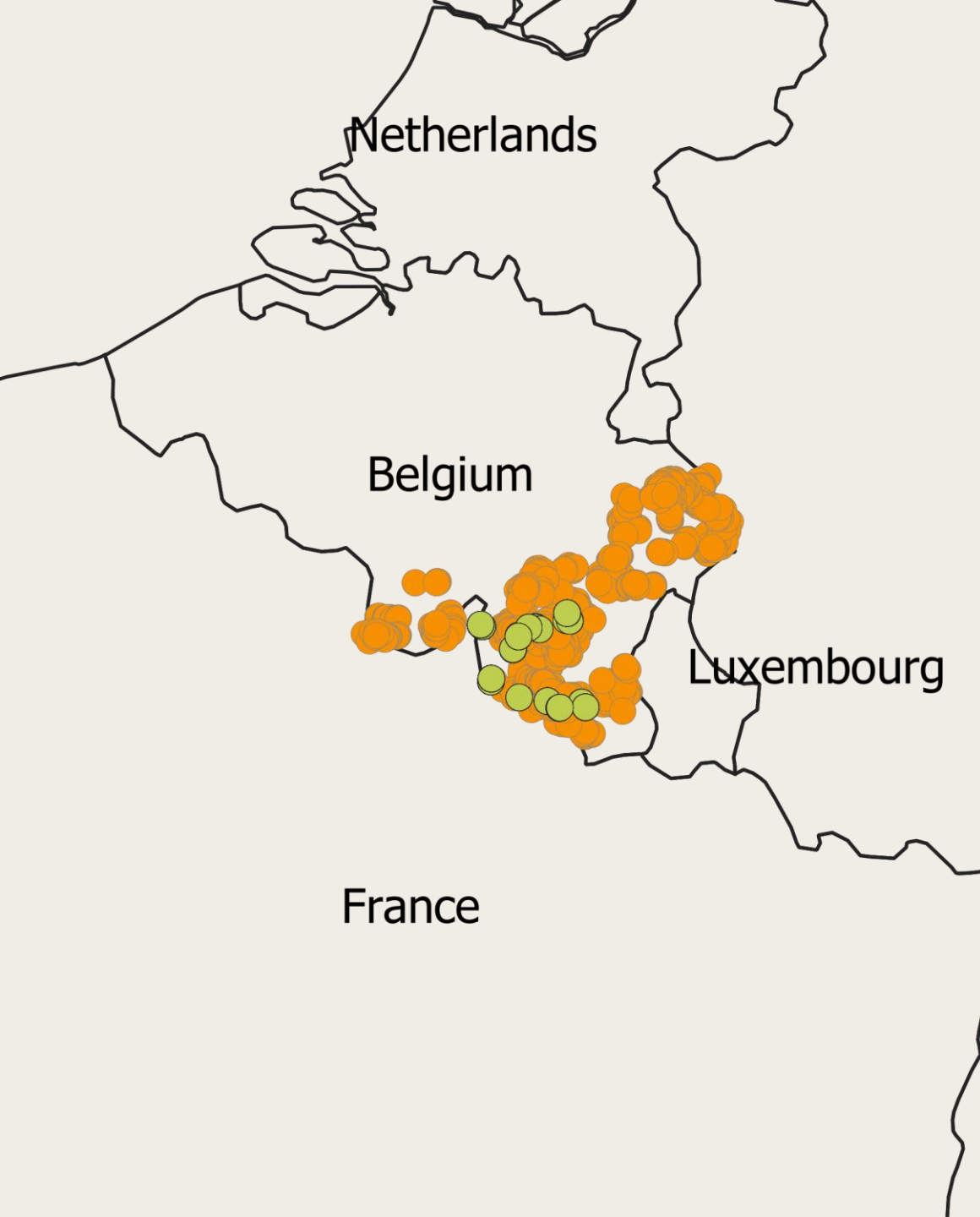
Switzerland



7.5 – 9.0 °C



800-1300 mm/year



Forests on **mesic acidophilous** sites dominated by broadleaved species and managed with **continuous cover forestry**.

**Main species with different shade tolerance :**

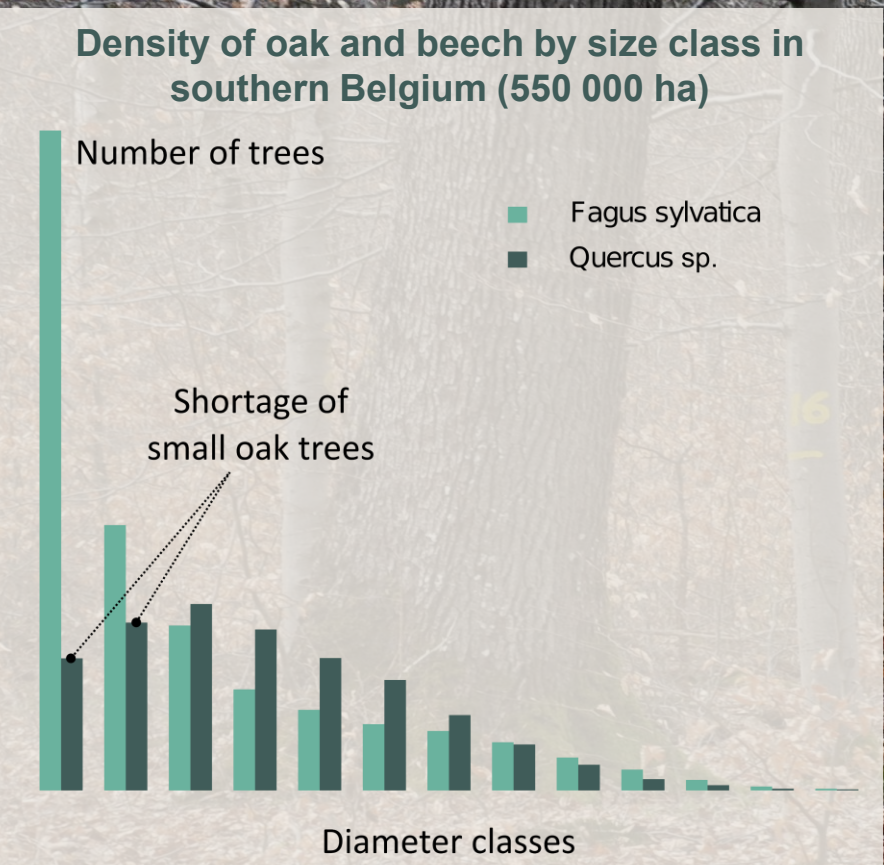
- Fagus sylvatica* (beech)
- Picea abies* (spruce)
- Carpinus betulus* (hornbeam)
- Acer pseudoplatanus* (sycamore maple)
- Quercus petraea* (sessile oak)
- Fraxinus excelsior* (ash)
- Quercus robur* (pedunculata oak)
- Betula pendula, Betula pubescens* (birch)



Can we promote the natural regeneration of oak? What are the light conditions that best promote species diversity?

Sessile oak  
*Quercus petraea* (Matt) Liebl.  
  
Less shade-tolerant  
Scarce in natural regeneration

European beech  
*Fagus sylvatica* L.  
  
Shade-tolerant  
Invade the understory






Forests on **mesic acidophilous** sites with coniferous plantation species and managed with **continuous cover forestry** conversion into unevenaged stand

**Main species with different shade tolerance :**

- Fagus sylvatica* (beech)
- Picea abies* (spruce)
- Pseudotsuga menziesii* (Douglas-fir)
- Larix* sp. (Larch)



 7.5 – 9.0 °C

 800-1300 mm/year

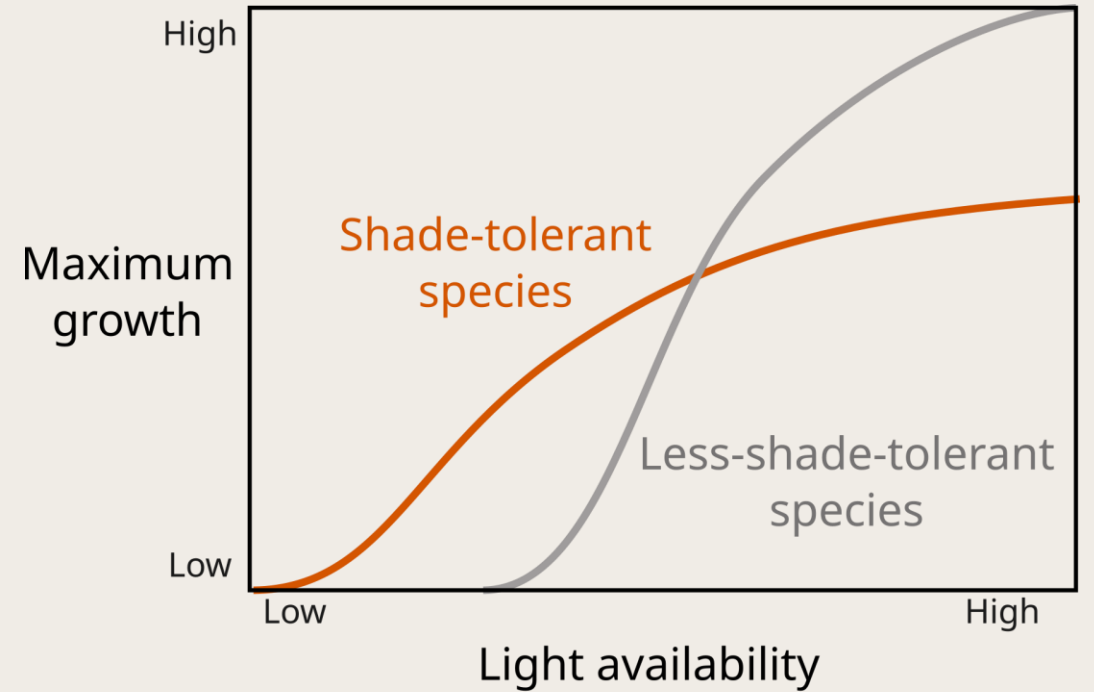
**Can we expect that tree species diversity will increase in stands managed without clear-cut? What are the light conditions that best promote species diversity? Can we control it?**



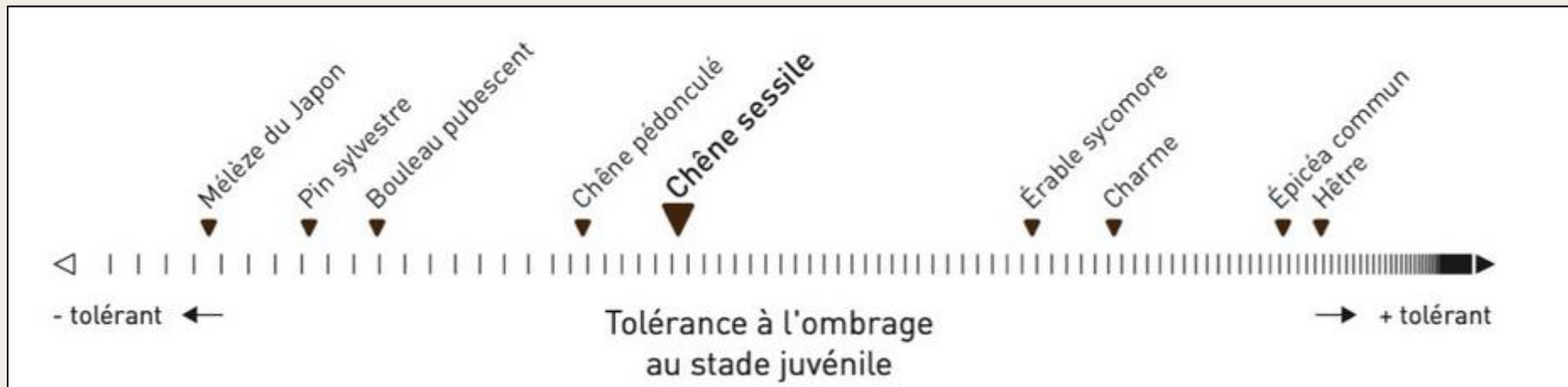
A photograph of a forest with sunlight filtering through the trees, creating a hazy, dappled light effect. The trees are tall and thin, with green foliage. The light is soft and diffused, creating a serene atmosphere.

Controlling regeneration diversity by regulating canopy openness (in forests managed under CCF)

Assuming a trade-off between survival at low-light conditions and maximum growth at high-light conditions, it should be possible to steer regeneration composition controlling understory light through targeted felling



adapted from Smith et Huston (1989) *Vegetatio* 83:49-69





27 fenced sites

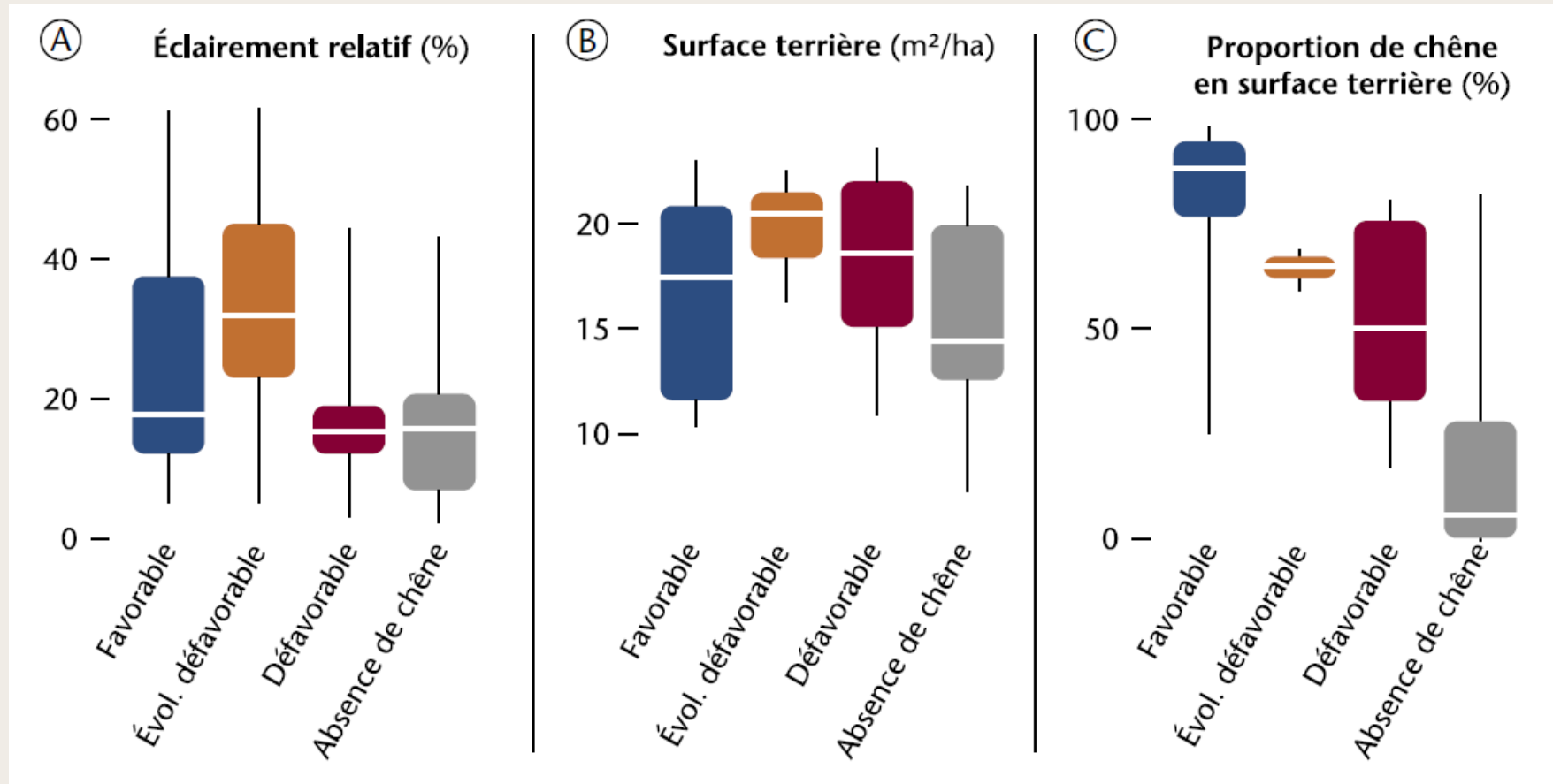
From early successional  
oak forests to late  
successional beech  
forests



Height of the 3 tallest saplings.  
Repeated measurements during  
3 years.

Hemispherical photographs to  
estimate the percentage of above  
canopy light (PACL) transmitted  
to the understory.

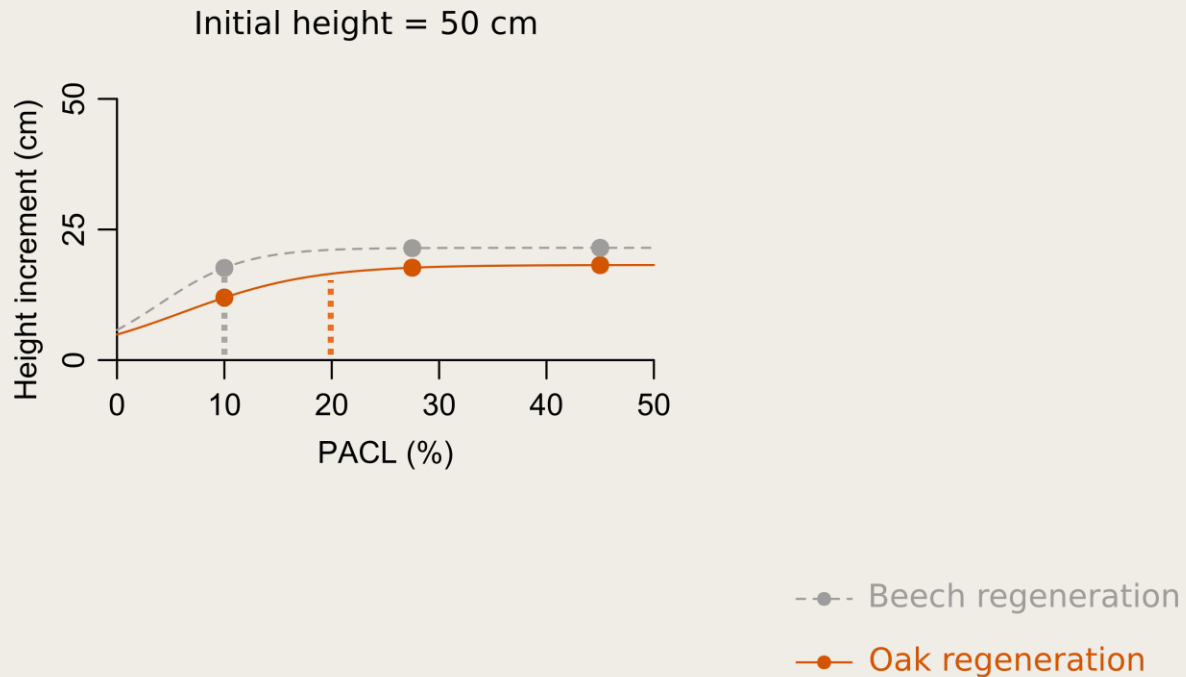
# Oak regeneration success depended primarily on the abundance of adult oak trees



LIGOT et al. 2014, Forêt Wallonne. 128

Also demonstrated by : Dietz et al. 2022 Forest Ecology and Management, 503; Petritan et al. 2012 Forest Ecology and Management, 280 ; Annighöfer et al (2015) Plos one

# Beech regenerations grow faster than oak regenerations whatever the light conditions



- Importance of initial sapling height
- No tradeoff between survival in shade and growth in high-light condition
- Oak saplings needs twice as much light as beech saplings to reach their full growth potential
- Optimum light : 20 – 40% of above canopy light

# Many similar observations in different forests

Annals of Botany 112: 1421–1430, 2013  
doi:10.1093/aob/mct200, available online at www.aob.oxfordjournals.org

ANNALS OF  
BOTANY  
founded 1857

## Light and competition gradients fail to explain the coexistence of shade-tolerant *Fagus sylvatica* and shade-intermediate *Quercus petraea* seedlings

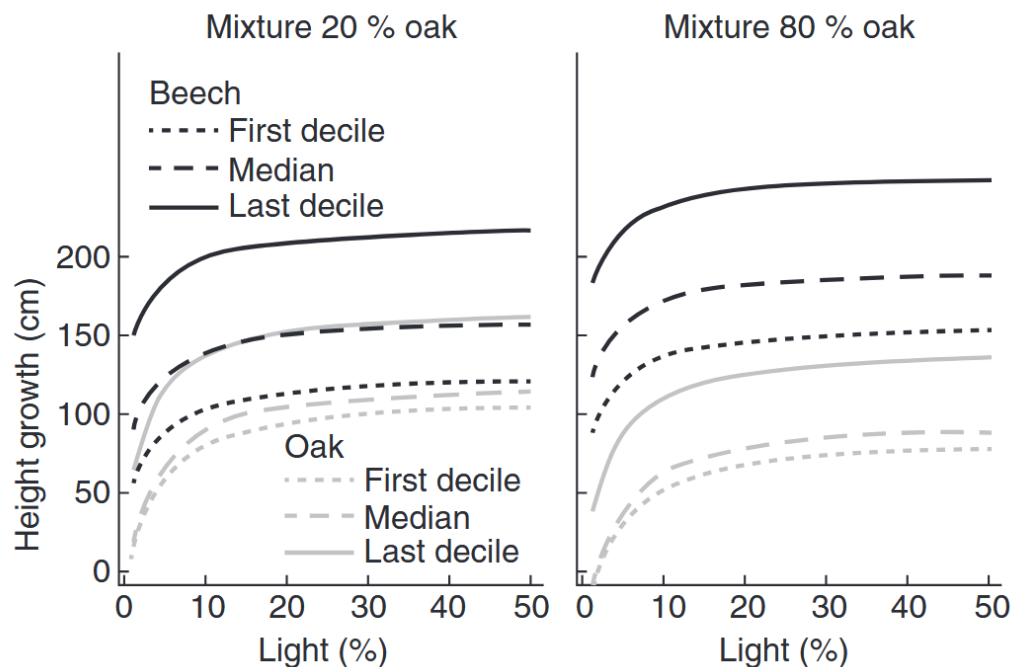
Rosalinde Van Couwenberghe<sup>1,2,\*</sup>, Jean-Claude Gégout<sup>1,2</sup>, Eric Lacombe<sup>1,2</sup> and Catherine Collet<sup>1,2</sup>

<sup>1</sup>INRA, UMR1092, Laboratoire d'Etude des Ressources Forêt Bois, Centre de Nancy, 54280 Champenoux, France and

## Uneven-aged oak-beech stand in France (Lorraine)

- Storms opened the canopy
- Light gradient : 5-50%
- Initially, some beech seedlings were taller than oak seedlings

“No rank reversal occurs between the two species along the light gradient [...] spatial heterogeneity in canopy opening [does not explain] the coexistence of the two species studied”



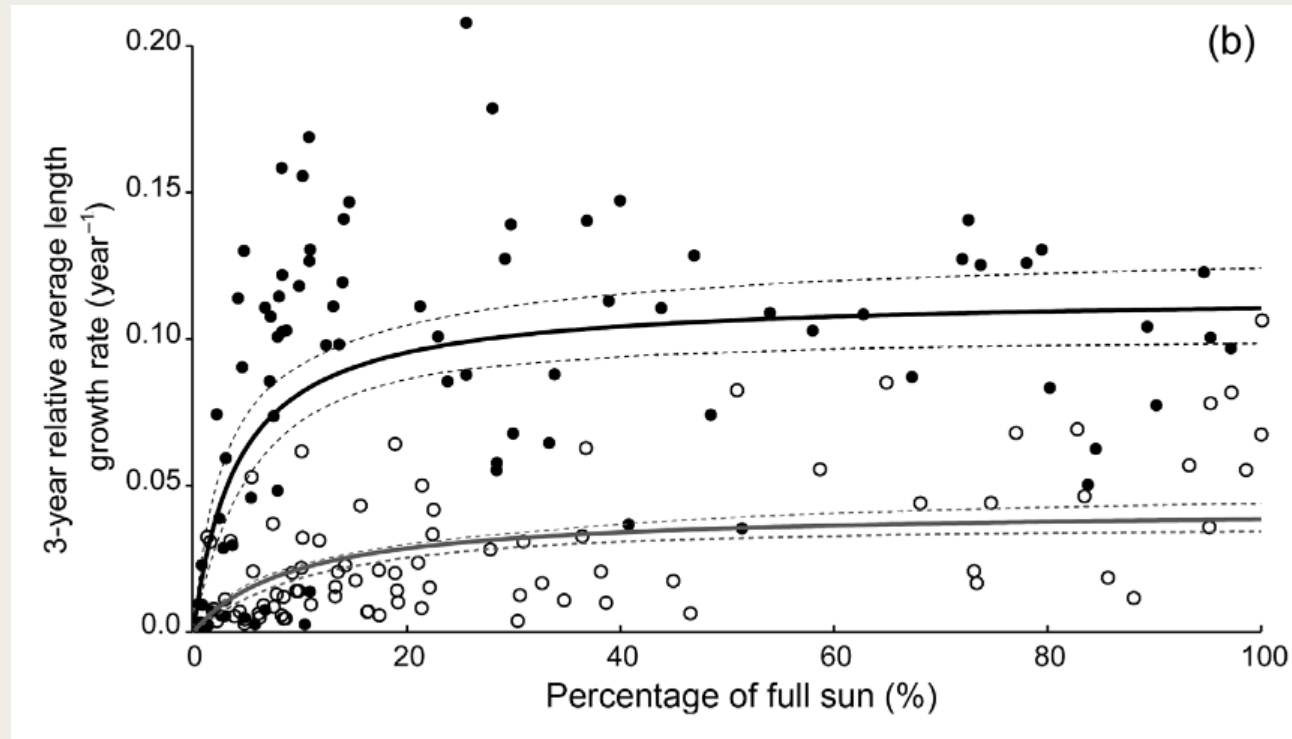
# Many similar observations in different forests

Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest

Georges Kunstler, Thomas Curt, Monique Bouchaud, and Jacques Lepart

Downy oak-beech-pine forest in **France** (Causse du Larzac)

“beech has a better growth and survival than oak at a high light regime. This is not in agreement with the mortality–growth trade-off”



Beech

Downy oak (*Q. pubescens*)

# But also, some different observations

Forest Ecology and Management 503 (2022) 119758

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: [www.elsevier.com/locate/foreco](http://www.elsevier.com/locate/foreco)



Beech and hornbeam dominate oak 20 years after the creation of storm-induced gaps

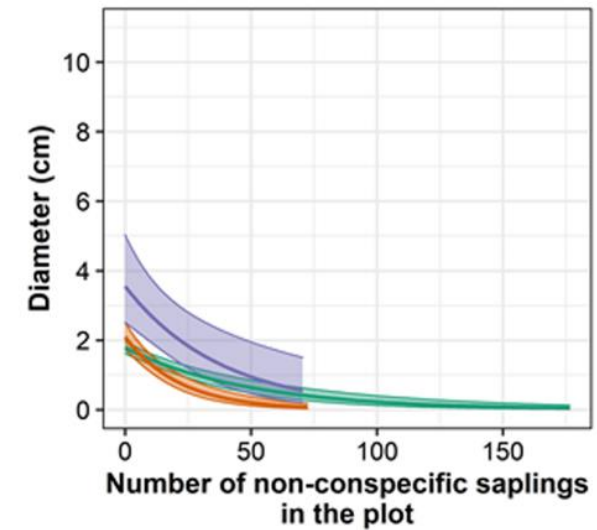
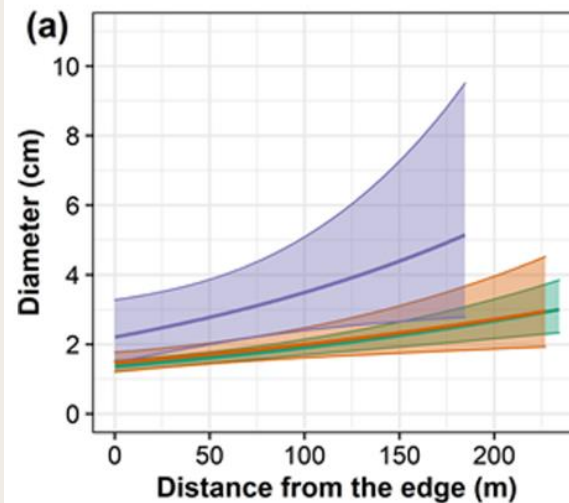
Lucie Dietz<sup>a,b,\*</sup>, Jean-Claude Gégout<sup>a</sup>, Jean-Luc Dupouey<sup>a</sup>, Eric Lacombe<sup>a</sup>, Lisa Laurent<sup>a</sup>, Catherine Collet<sup>a</sup>

<sup>a</sup> Université de Lorraine, AgroParisTech, INRAE, UMR Siva, 54000 Nancy, France  
<sup>b</sup> Office National des Forêts, 54000 Nancy, France

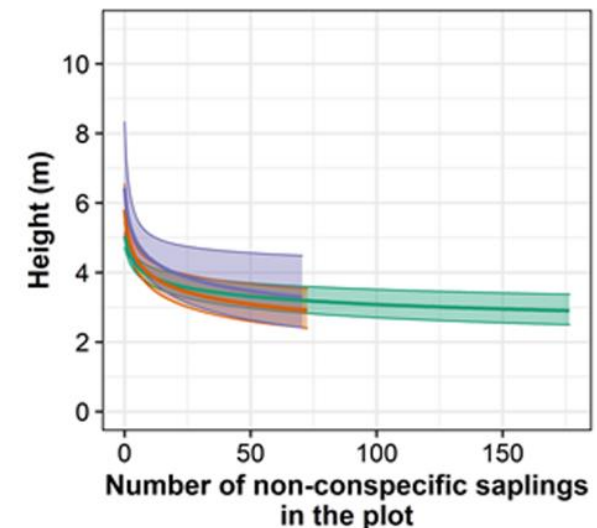
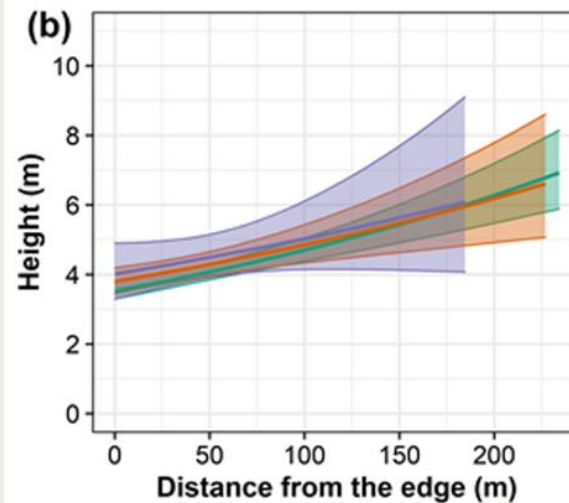
## Inventory in storm-induced gaps (20 years after the storm) in France

- 1153 plots, 108 gaps (with some gaps > 1 ha)
- Saplings of oak, beech, hornbeam
- No silvicultural treatment during 20 years

“Unlike Ligot et al., (2013), Van Couwenberghe et al. (2013) or Tinya et al. (2020), we did not observe a dominance of beech or hornbeam over oak DBH or height, showing that oak saplings were not overtopped 20 years after opening.”



Saplings



# But also, some different observations

European Journal of Forest Research (2020) 139:41–52  
<https://doi.org/10.1007/s10342-019-01238-7>

ORIGINAL PAPER

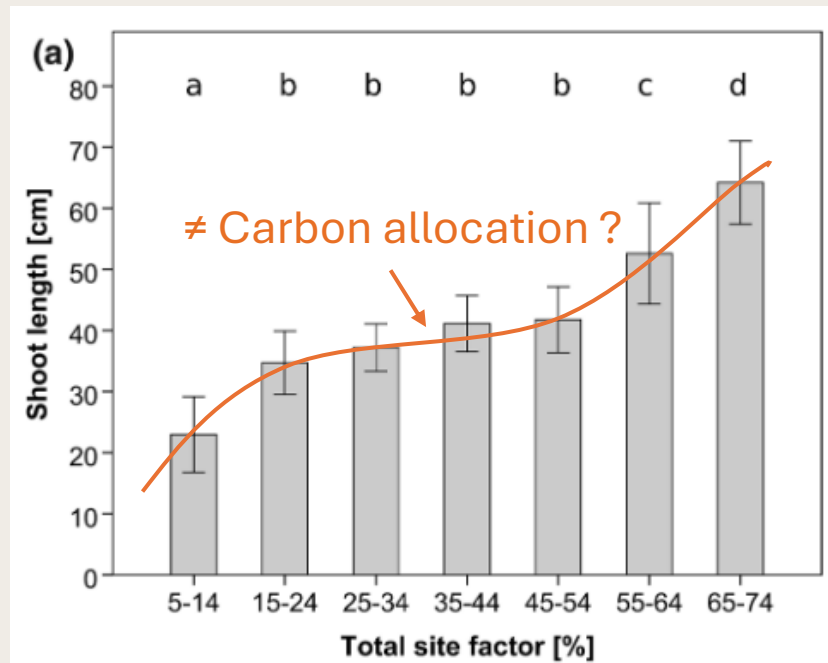


Photosynthetic performance, height growth, and dominance of naturally regenerated sessile oak (*Quercus petraea* [Mattuschka] Liebl.) seedlings in small-scale canopy openings of varying sizes

Tobias Modrow<sup>1</sup> · Christian Kuehne<sup>3</sup> · Somidh Saha<sup>2</sup> · Jürgen Bauhus<sup>1</sup> · Patrick L. Pyttel<sup>1</sup>

160 year-old oak stand with an under- and midstory of beech and hornbeam in **Germany** (Heilbronn).

- Managers opened gaps of varying size (0.05-0.2 ha)
- Light gradient : 5-75 %
- Oak and beech seedlings were initially of about the same size (20 cm).



“at relative radiation levels of close to 50% oak was able to compete with or even outgrow shade-tolerant species while shade-intolerant species were still not competitive enough to dominate the regeneration layer”

# But also, some different observations

## Einfluss unterschiedlicher Hiebsformen auf die Naturverjüngung eines Traubeneichen-Buchen-Mischbestandes

– Der Versuch „Mastlager“ der Forschungsanstalt für Waldökologie und Forstwirtschaft Rheinland-Pfalz im Forstamt Wasgau (früher Eppenbrunn) –

**Burghard von Lüpke**

Institut für Waldbau der Universität Göttingen

2008

### Abstract

#### Title of the paper:

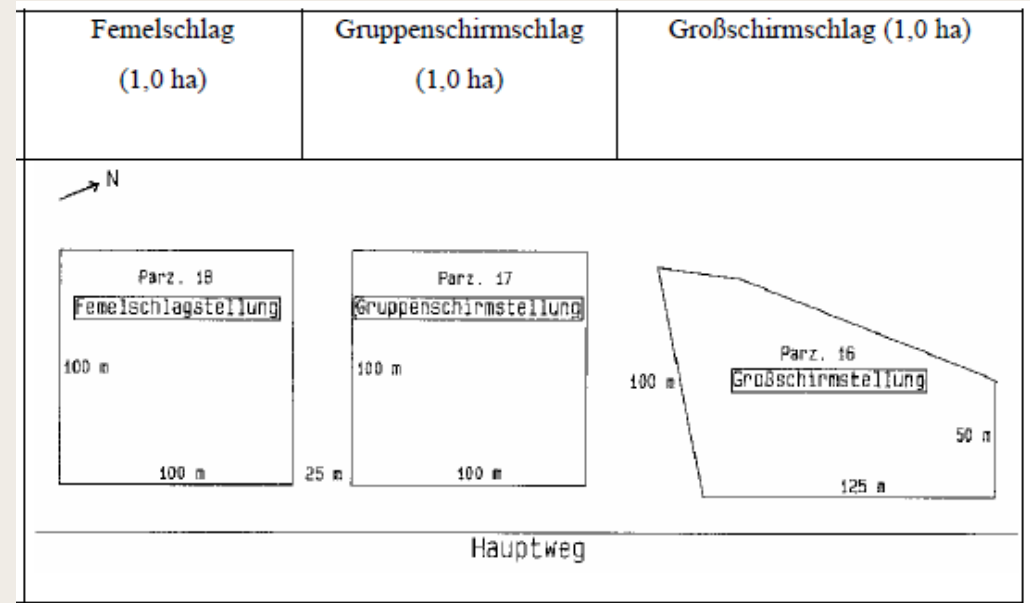
Influence of various cutting types on natural regeneration of a sessile oak – beech mixed stand. – The experiment “Mastlager” of the Research Institute for Forest Ecology and Forestry Rhineland-Palatinate in the district Wasgau (formerly Eppenbrunn) –

300 year-old oak-beech stand in **Germany** (Heilbronn).

Treatment : 3 cutting types to release oak regeneration after mast year 1989 (Irregular shelterwood, group shelterwood, uniform shelterwood)

- Light gradient : 27-67%

Oak saplings grew faster than beech when PACL > 38% after 5 years and PACL > 50% after 8 years

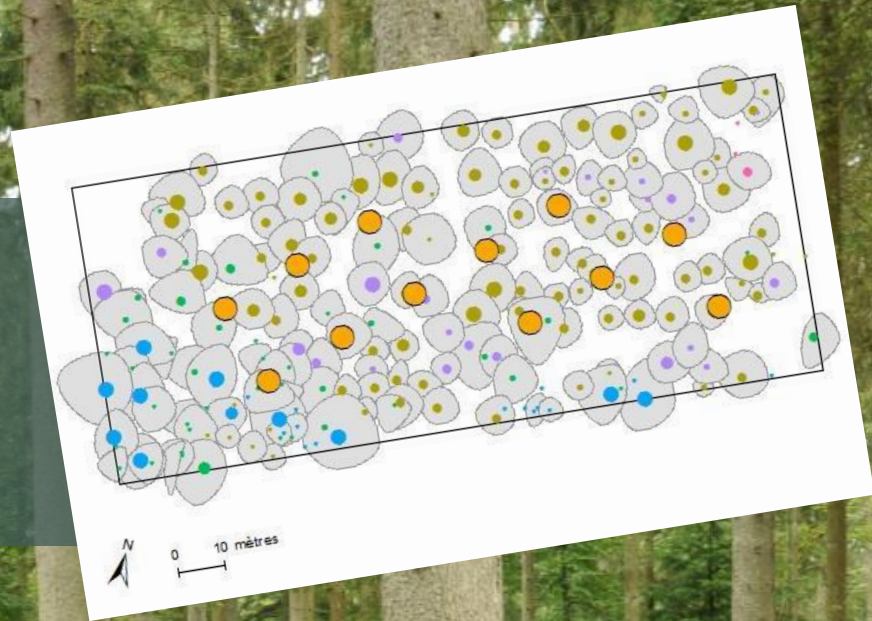




# 9 coniferous stands in Belgium at 400-600 m a.s.l



- 1 ha plots in each site
- 12 circular subplots of 3-m radius



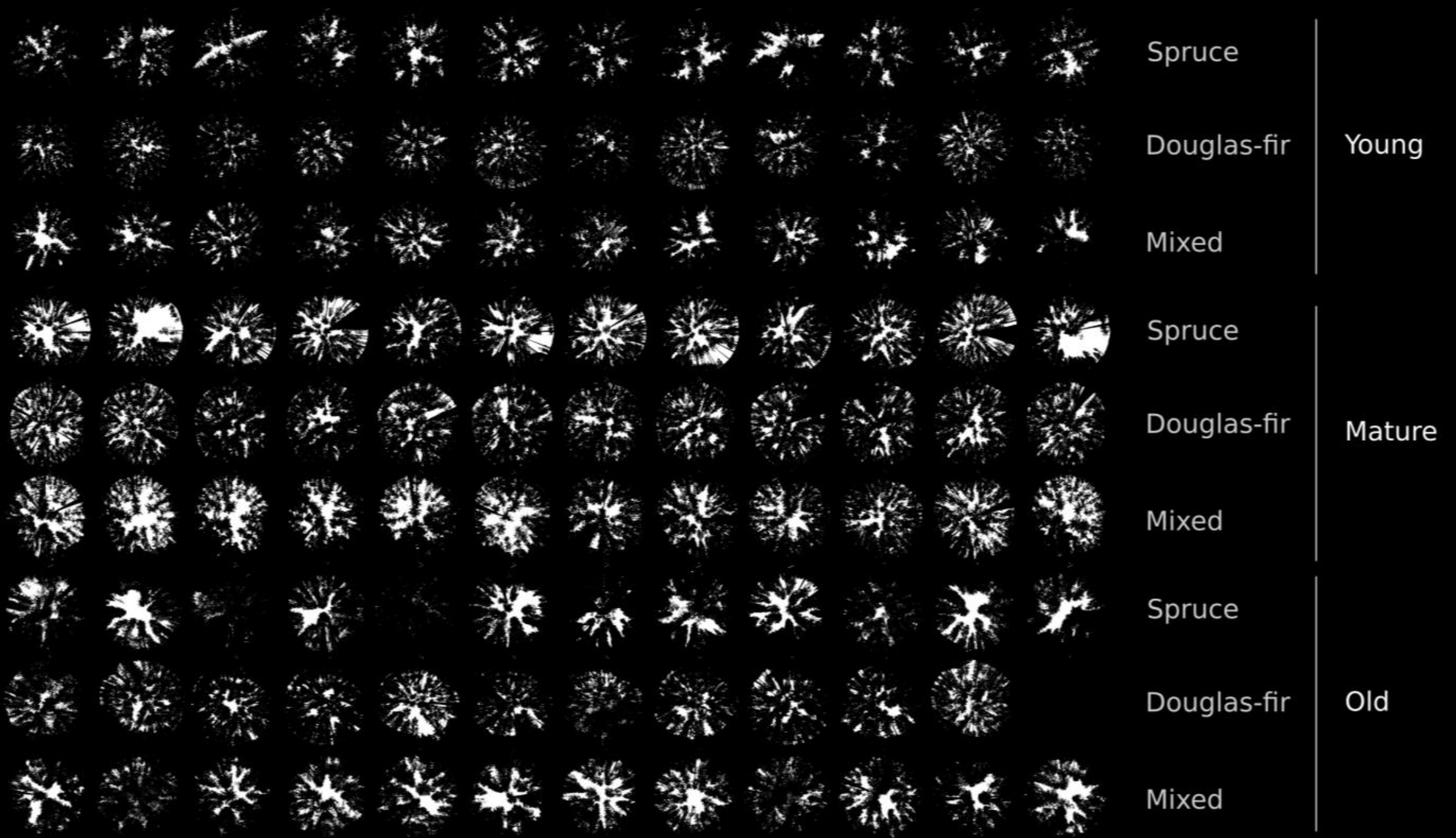
2



For the 3 tallest saplings of each species, we measured

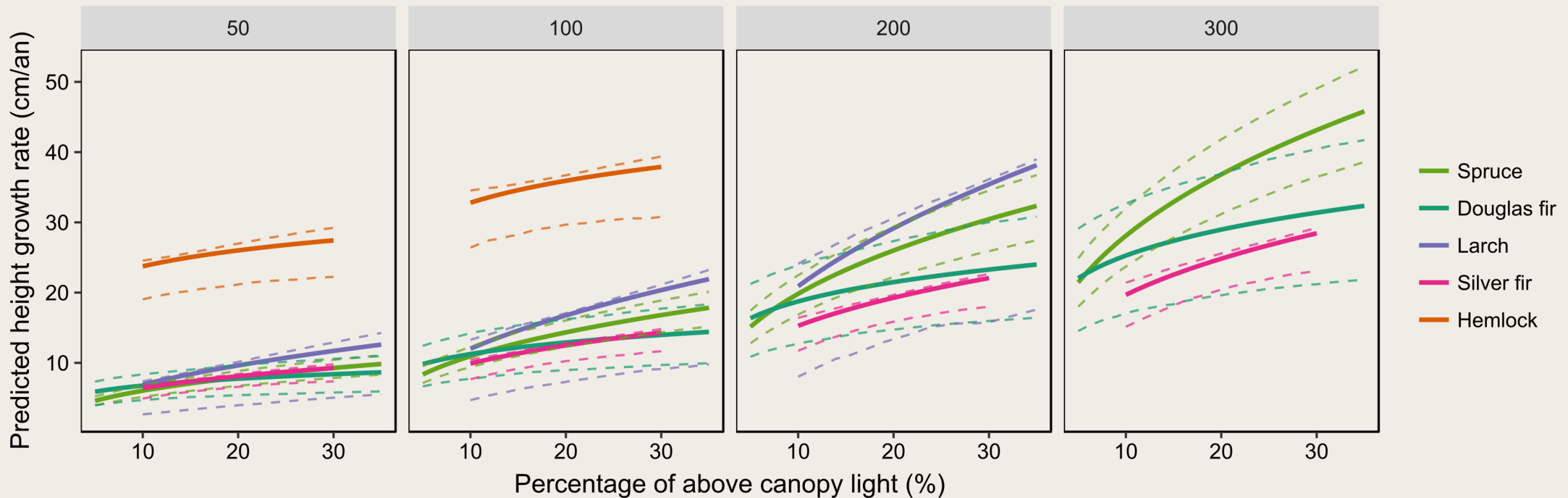
- Sapling height
- Terminal shoots
- ...





# The ranking of species based on height growth was the same under all lighting conditions

- Height increment increased with sapling height
- Western hemlock grew three times faster than the other species

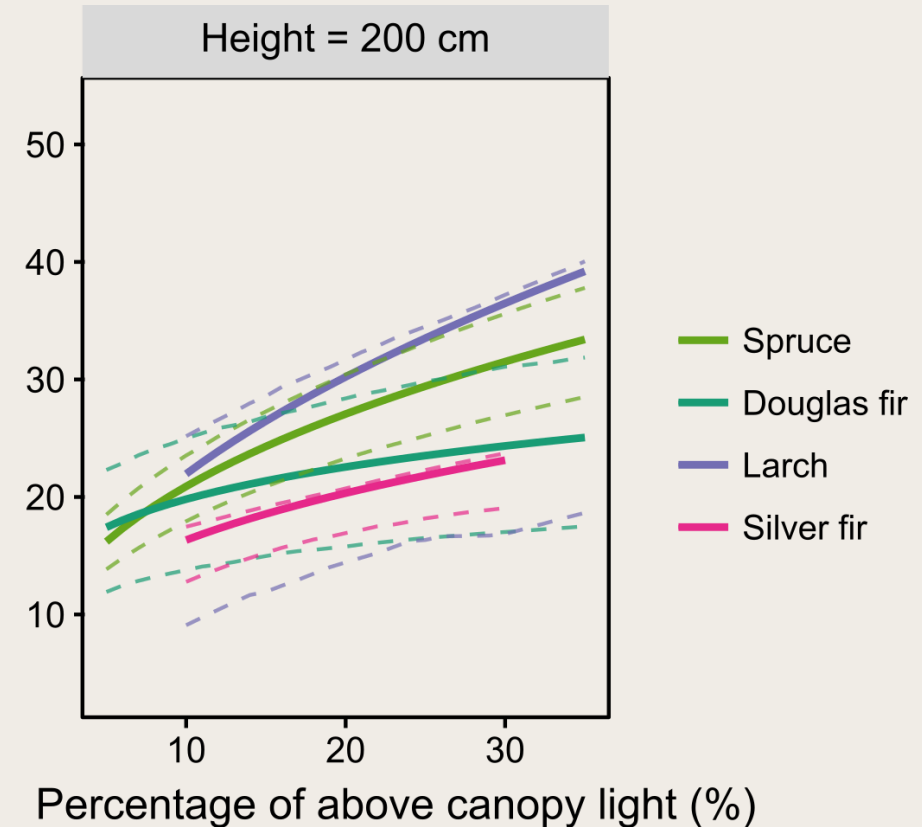


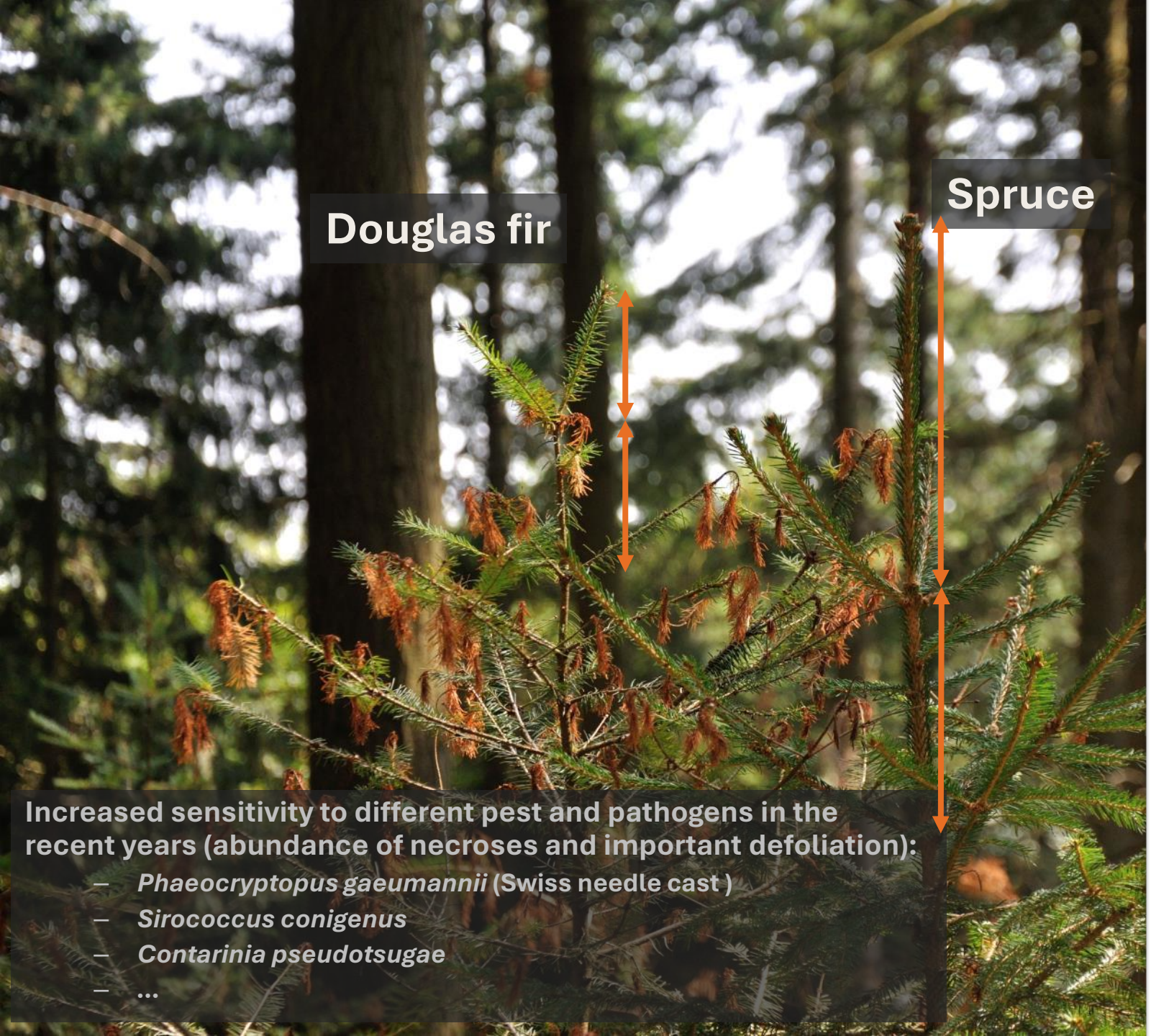
# The ranking of species based on height growth was the same under all light conditions

By order of decreasing height increment:

1. Larch (shade intolerant)
2. Spruce (shade tolerant)
3. Douglas fir (less shade tolerant)
4. Silver fir (very shade tolerant)

Predicted  
height increment  
(cm/year)





**Douglas fir**

**Spruce**

**Increased sensitivity to different pest and pathogens in the recent years (abundance of necroses and important defoliation):**

- *Phaeocryptopus gaeumannii* (Swiss needle cast)
- *Sirococcus conigenus*
- *Contarinia pseudotsugae*
- ...



# Overall, weak niche partitioning over the studied light gradients

Similarly, gap size has been showed<sup>1</sup> to be a poor predictor of recruitment composition, especially to predict the regeneration success of less-shade tolerant species.



1. Busing and White (1997) *Oikos* 78 ; Coates (2002) *For. Ecol. Manag.* 155 ; De Römer et al. (2007) *J. Veg. Sci.* 18 ; Nagel et al. (2010) *Plant Ecol.* 208

# Interspecific competition depends on multiple factors

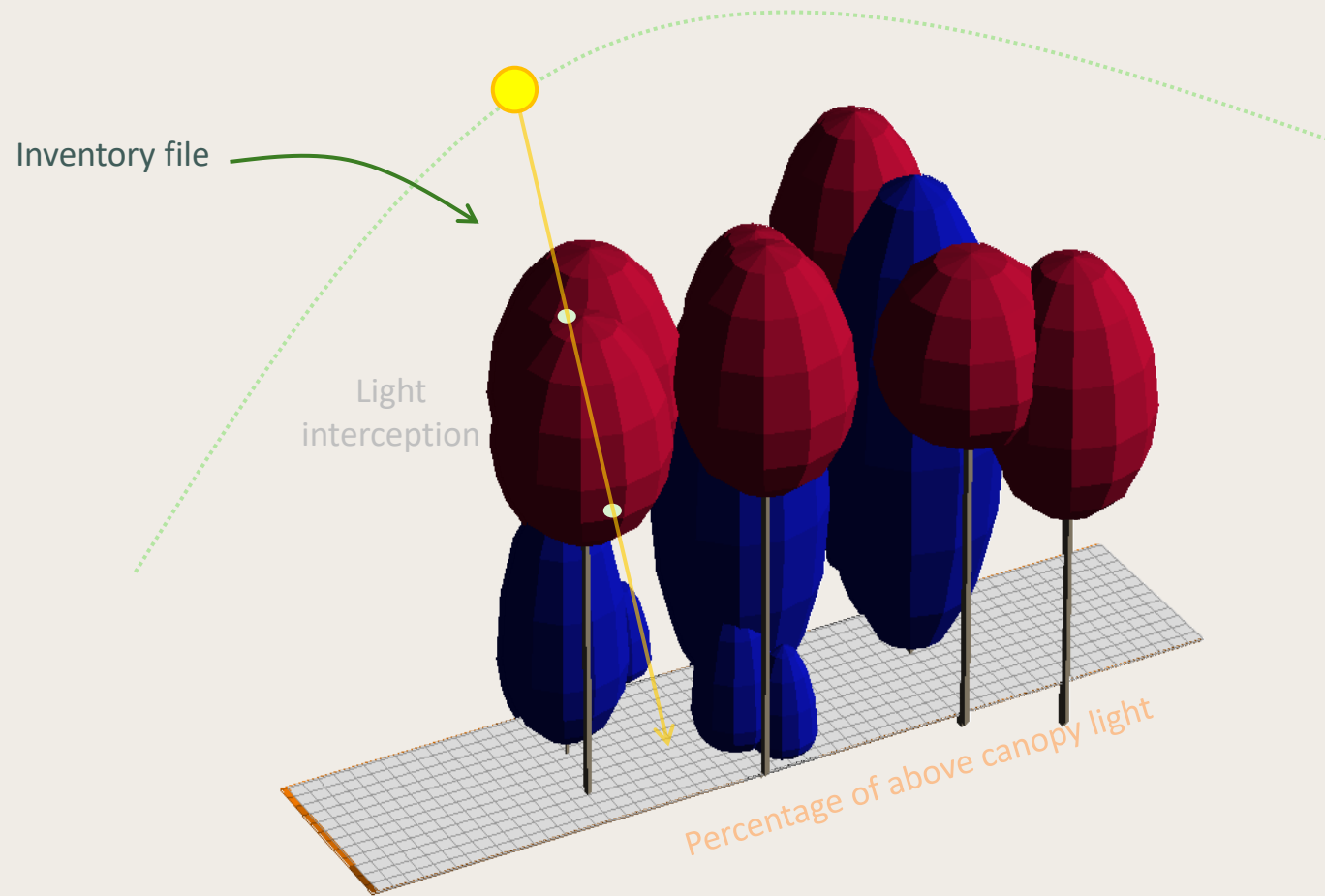
- Light is one abiotic factors among others (Temperature, water and nutrient availability....)
- Management history (stand composition)
- Difference in initial height (presence of advanced saplings)
- Herbivores (ungulates)
- Pest and pathogens
- ...



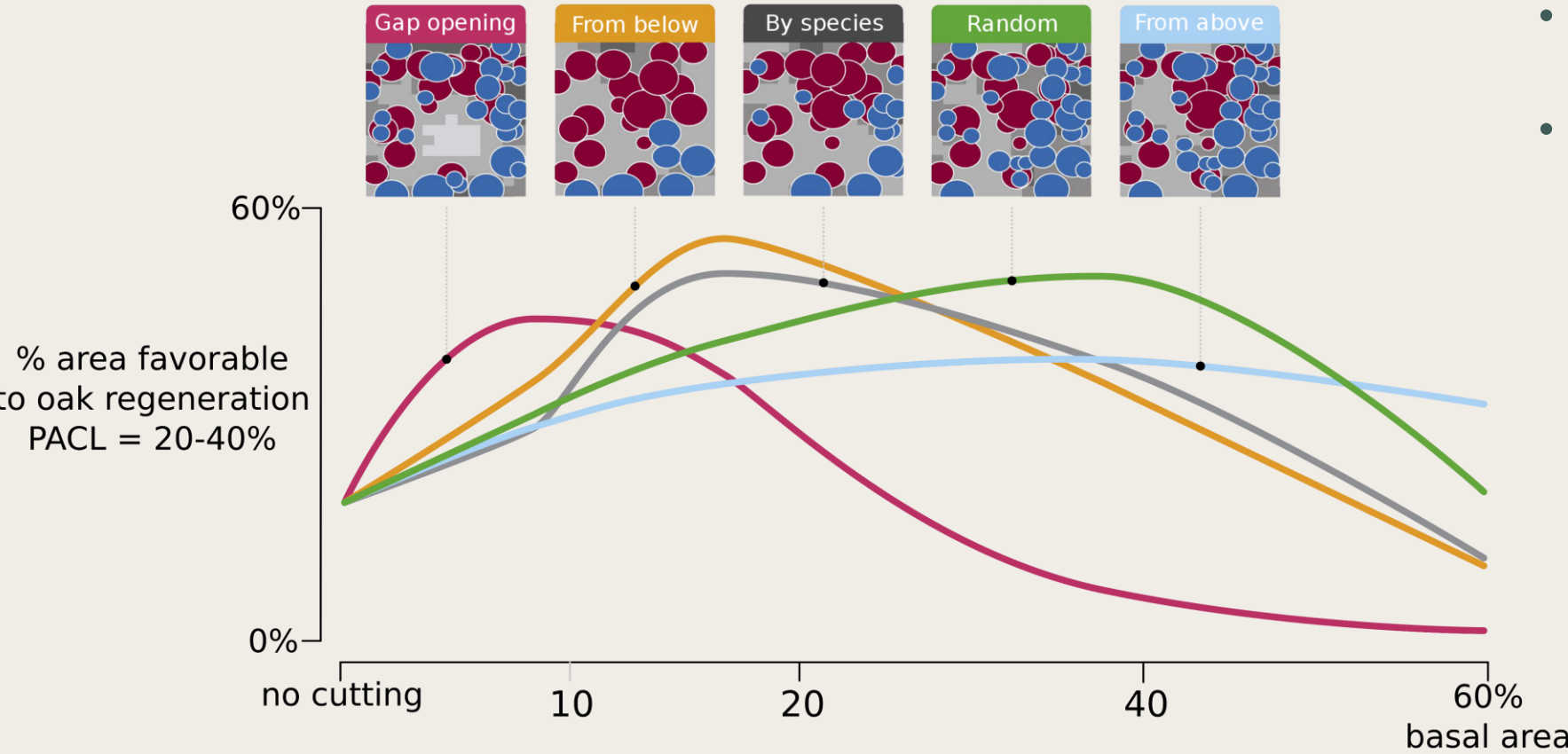
**Under CCF, to control recruitment composition, forest manager must control canopy openness and implement silvicultural interventions**



# Modeling light interception



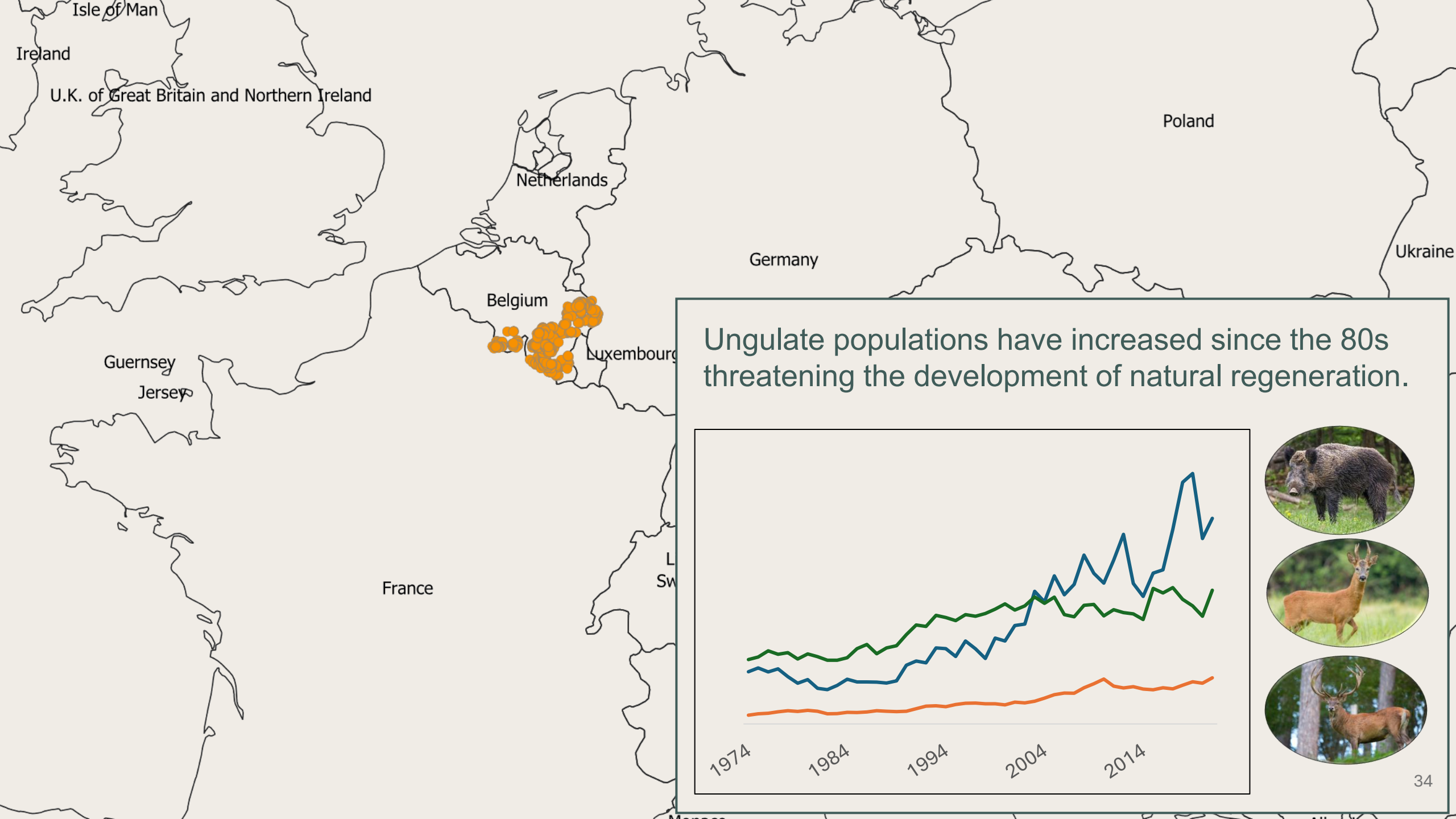
# Simulating different silvicultural options to promote oak regeneration



- Opening small gaps (<500 m<sup>2</sup>)
- Cutting preferentially small trees and trees of shade tolerant species maximized the area favorable to oak

- How much ungulates reduce regeneration height growth ?
- How much ungulates affect future stand diversity under CCF?





Ungulate populations have increased since the 80s threatening the development of natural regeneration.

The line graph displays three data series representing different ungulate populations over time. The x-axis shows years from 1974 to 2014. The top blue line shows a significant increase, peaking around 2014. The middle green line shows a steady increase. The bottom orange line shows a slight increase. To the right of the graph are three circular images of ungulates: a brown bear, a red deer, and a stag.

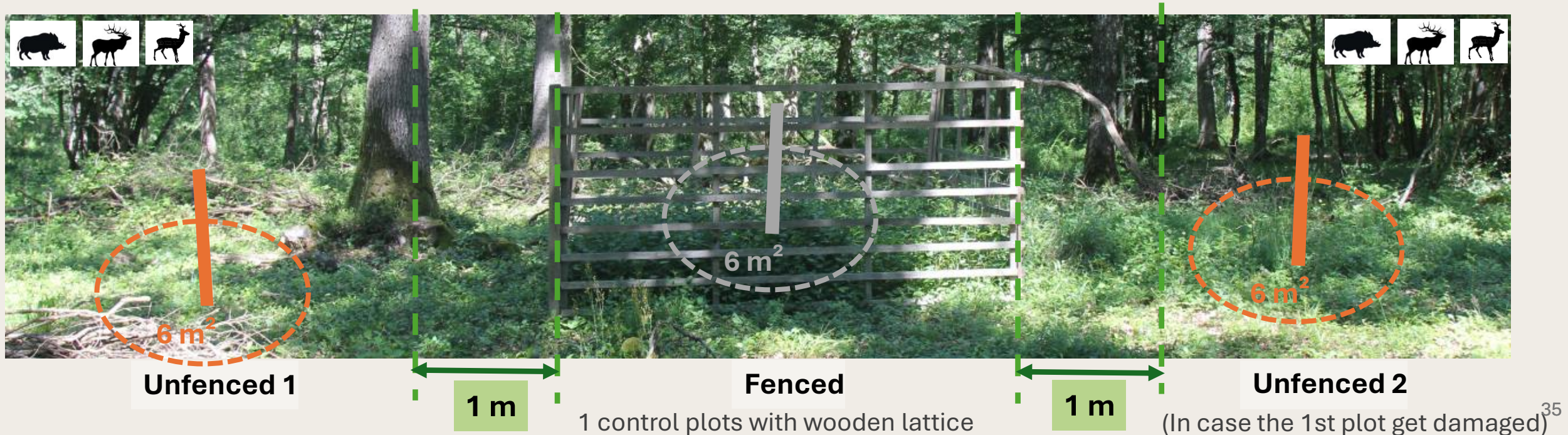
Year	Blue Line (Relative Population)	Green Line (Relative Population)	Orange Line (Relative Population)
1974	Low	Low	Low
1984	Low	Low	Low
1994	Medium	Medium	Low
2004	High	High	Low
2014	Very High	High	Low

# Monitoring natural regeneration in pairs of fenced-unfenced plots

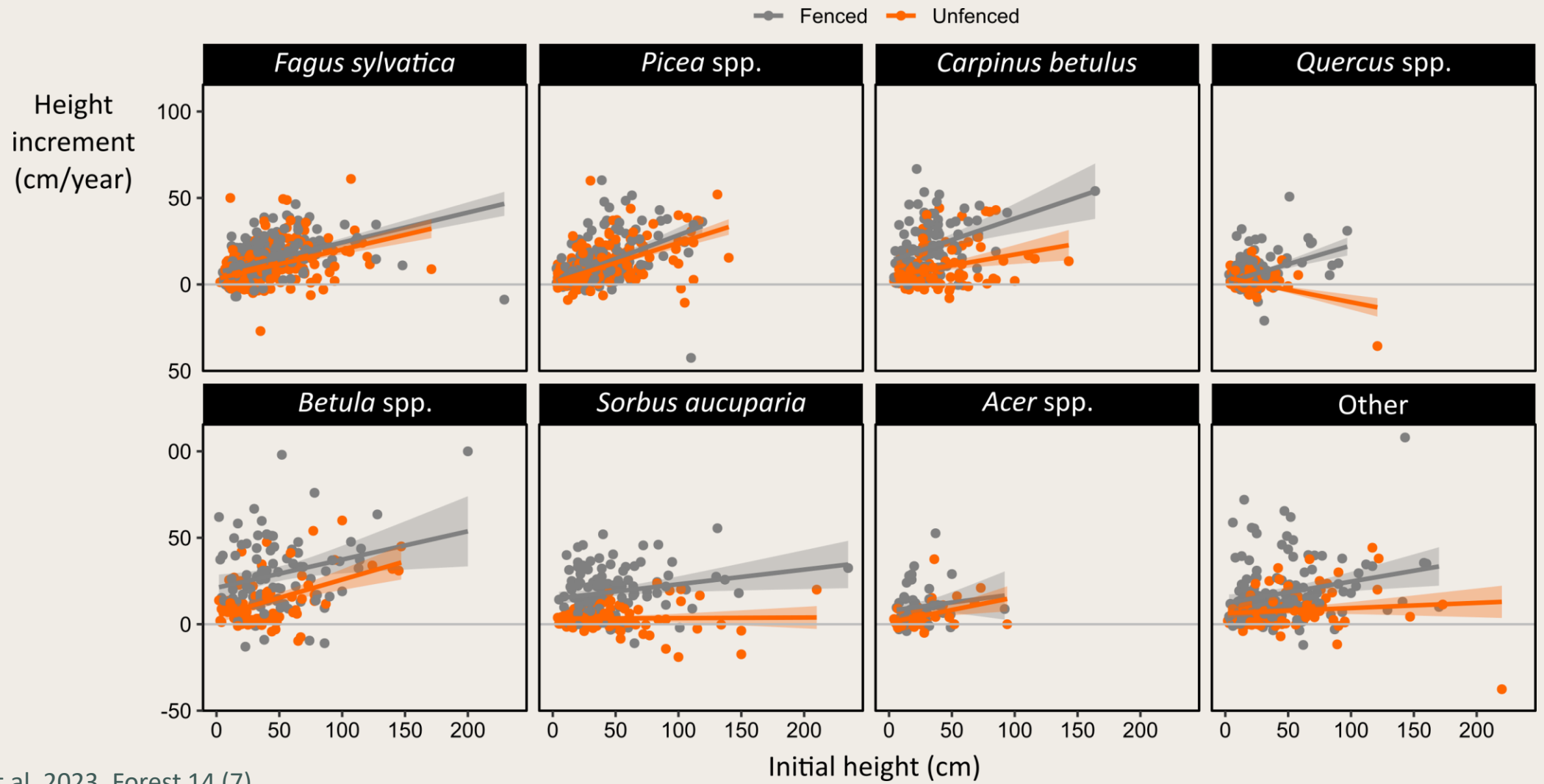
726 plot pairs (Systematic sampling) established where regeneration is not advanced but expected to be in good conditions (e.g. understory light) to thrive.



Annual monitoring (2016-2021) : Species identity and height of the 5 tallest seedlings ; Cover of woody/non-woody species.



Considering only the tallest saplings, the height increment of all species but beech and spruce was significantly reduced by browsing.



Species ranking in height increment was altered by browsing but oak was the slowest growing species in fenced and unfenced plots.

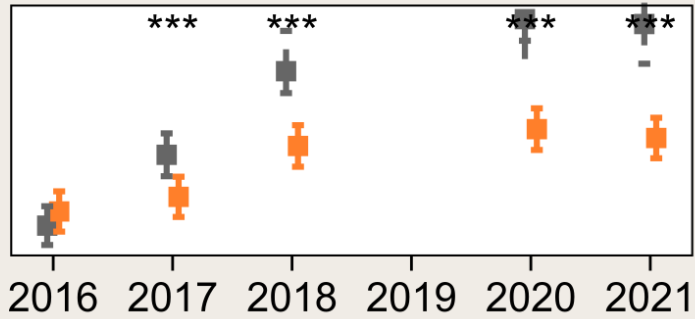
In fenced plots	
Species	iH (cm/yr)
Birch ( <i>Betula</i> sp.)	25
Rowan ( <i>Sorbus aucuparia</i> )	18
Hornbeam ( <i>Carpinus betulus</i> )	17
Beech ( <i>Fagus sylvatica</i> )	13
Maple ( <i>Acer pseudoplatanus</i> )	11
Norway spruce ( <i>Picea abies</i> )	10
Oak ( <i>Quercus</i> sp.)	7

Unfenced plots			
Species	iH (cm/yr)	$\Delta$ (cm/yr)	$\Delta$ (%)
Birch	10	15	60
Spruce	10	n.s.	n.s.
Beech	9	4	30
Hornbeam	6	11	65
Maple	5	6	54
Rowan	3	15	83
Oak	3	4	57

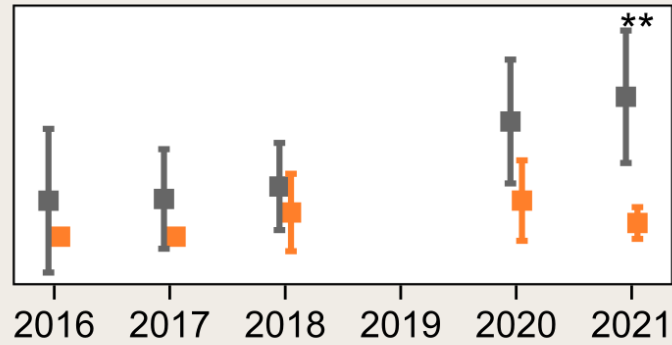
strongly suppressed species

Fenced
  Unfenced

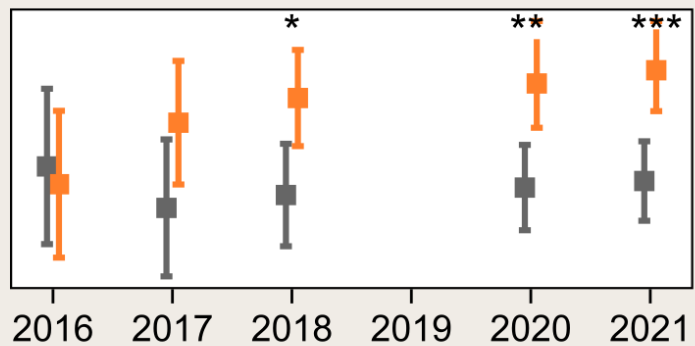
Shannon diversity index



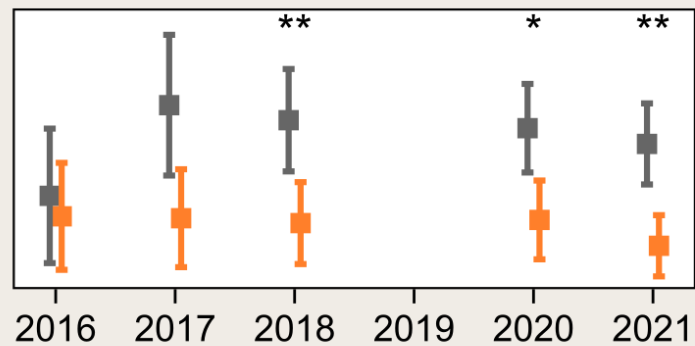
Temperature score



Humidity score



Light score



Years

Browsing reduced regeneration diversity, increased the share of shade tolerant species and species less-tolerant to warmer and drier conditions

## Broad

- Shade tolerance : ++
- Browsing resistant : ++
- Growth rate : +

Grow well in the understory, sit-and-wait strategy



## High light

- Shade tolerance : -
- Browsing resistant : --
- Growth rate : ++

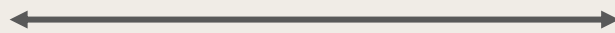
Grow well in large gaps and/or if ungulate pressure is low.



## Nowhere

- Shade tolerance : -
- Browsing resistant : -
- Growth rate : --

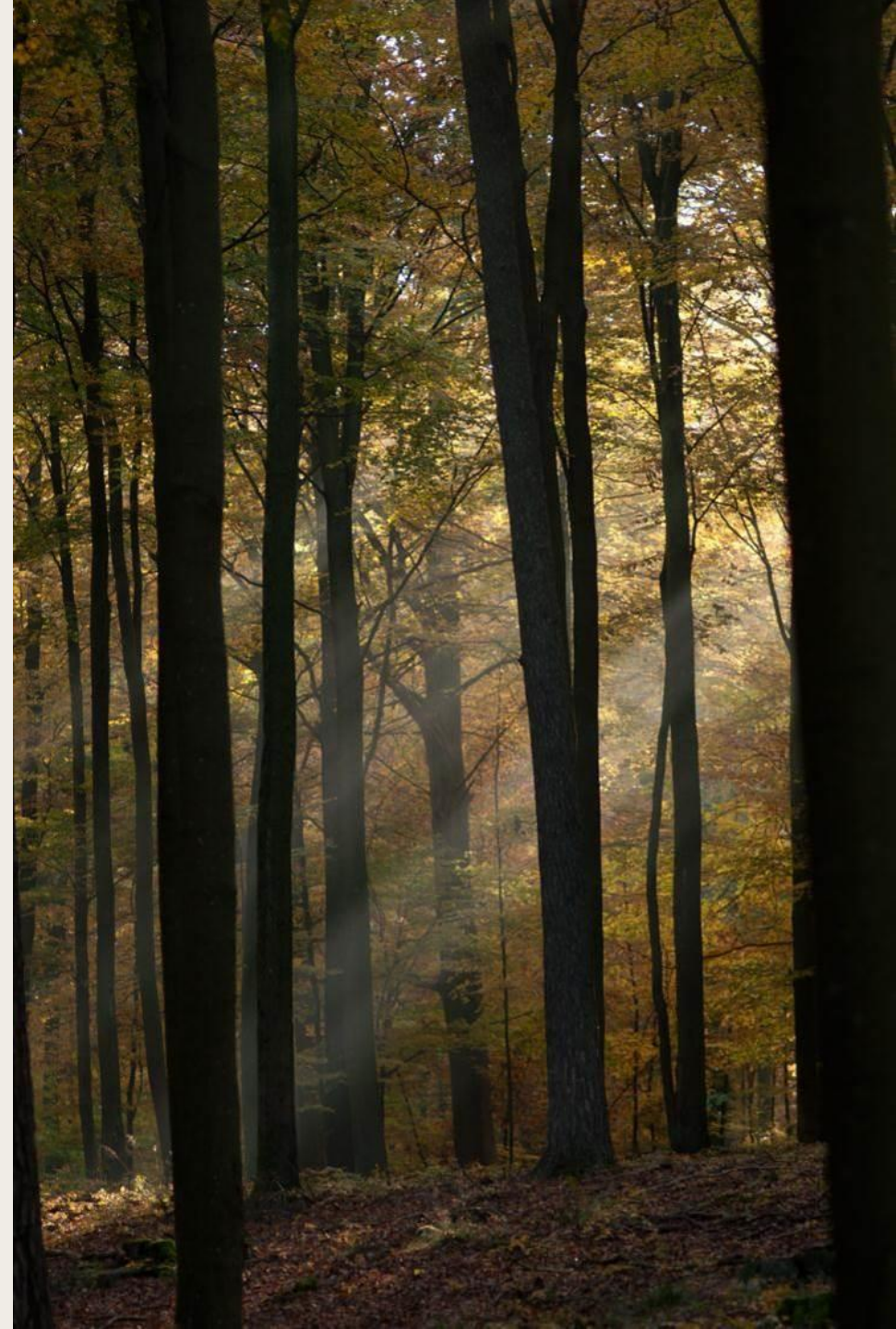
Do not regenerate easily, could regenerate better outside forests.



# Conclusions

Increasing forest diversity and forest resilience requires more than managing stand density and understory light availability.

Ungulate pressure can lead to a reduction in forest resilience to climate change. In some conditions, ungulates favor the late-successional species that are also less tolerant to dry and warm conditions.



# Call to action

- Compare **different silvicultural strategies** to promote regeneration diversity (with simulation tools and forest experiments).
- Investigate new solutions **at the landscape scale** as oak is known to regenerate profusely in transitional habitats (e.g. abandoned farmland) which requires allowing land use change.

Landscape Ecol (2018) 33:513–528  
<https://doi.org/10.1007/s10980-018-0619-y>



REVIEW ARTICLE

**Seeing the oakscape beyond the forest: a landscape approach to the oak regeneration in Europe**

Andrzej Bobiec · Albert Reif · Kinga Öllerer

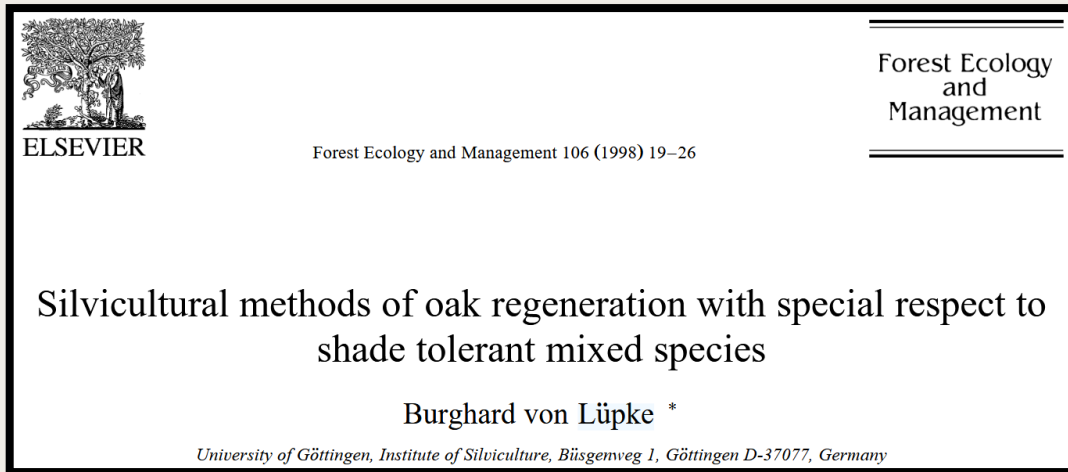




Thank you !



# Going back to the silvicultural recommendations of von Lüpke (1998)



Silvicultural recommendations to maintain mixed oak-beech stands in forests naturally dominated by beech (sub-Atlantic region of **Germany**)

- ✓ “**Initial height** has proved to be very important to the height increment within a particular period: plants which were initially larger had a greater increment.”
- ✓ “The oaks should have as great an age advantage as possible over the beeches; beeches should never originate from advanced growth.”
- ✓ “canopy covers, which allow between **40% and 10% of full light** to penetrate, transfer the competitive relationship more and more away from the oaks **in favour of the beeches.**”
- ✓ “Generally speaking, young oaks grow initially faster in clear cut areas than beech of the same age and achieve an advantage of 1–2 m within 30 years.” in Open area, beech saplings were affected by late frost whereas the oak were not affected.”
- ✓ “The regulation of inter-specific competition during cleanings and thinnings often necessitates great effort to maintain such a high number of oaks”