



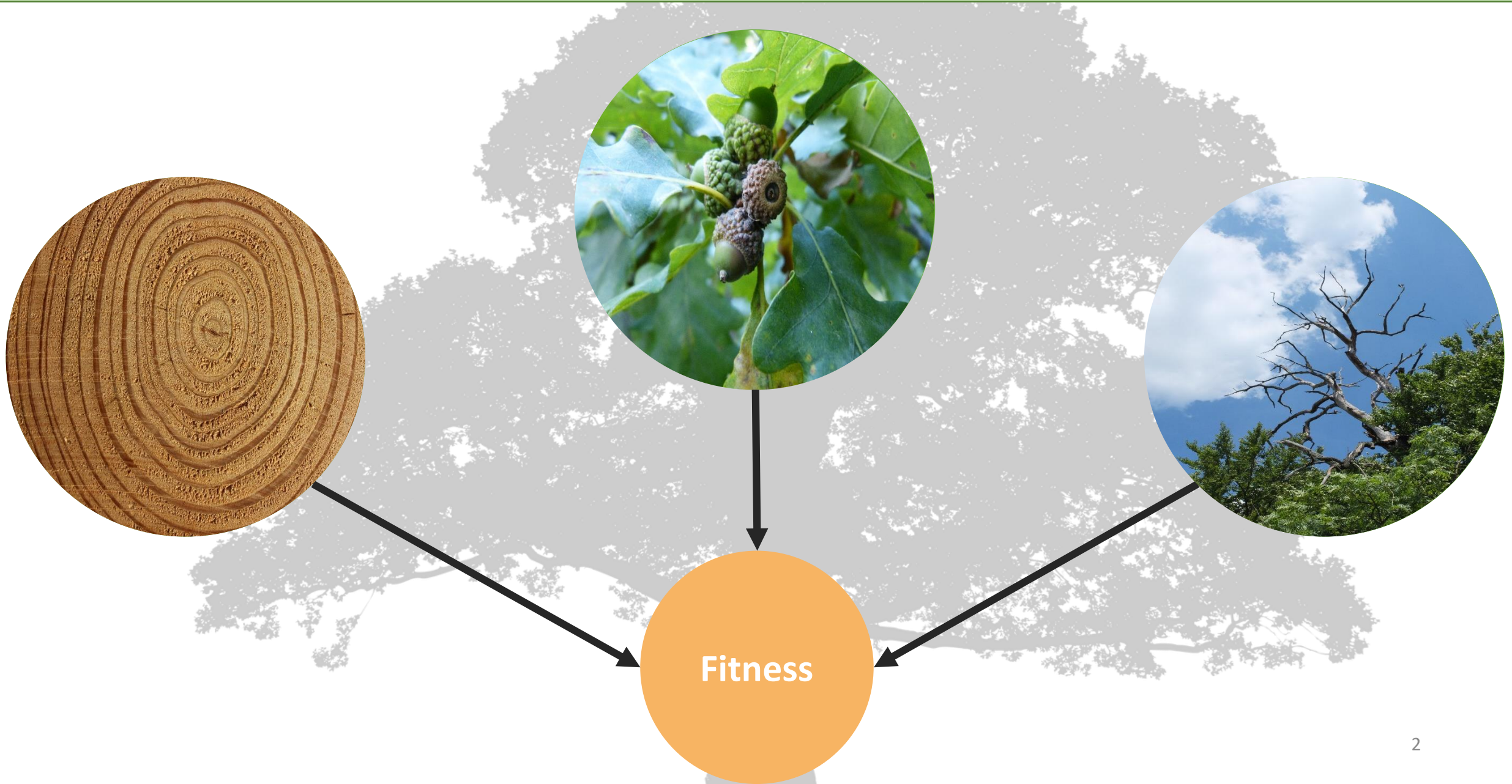
Ecologie fonctionnelle de la reproduction des plantes: Causes ultimes et proximales du phénomène de **masting**

THOMAS CAIGNARD – 21/11/2022

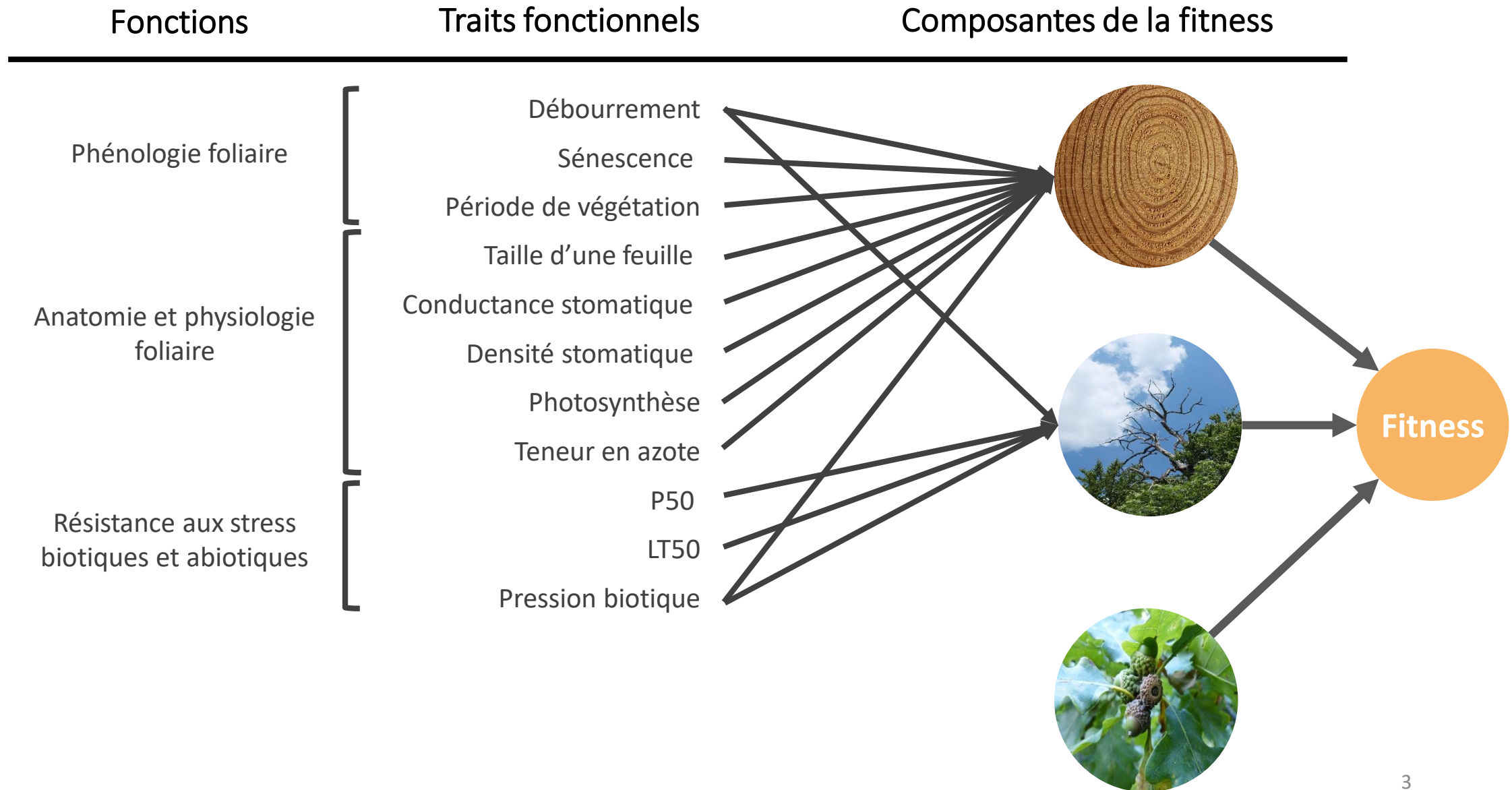
tcaignard@gmail.com



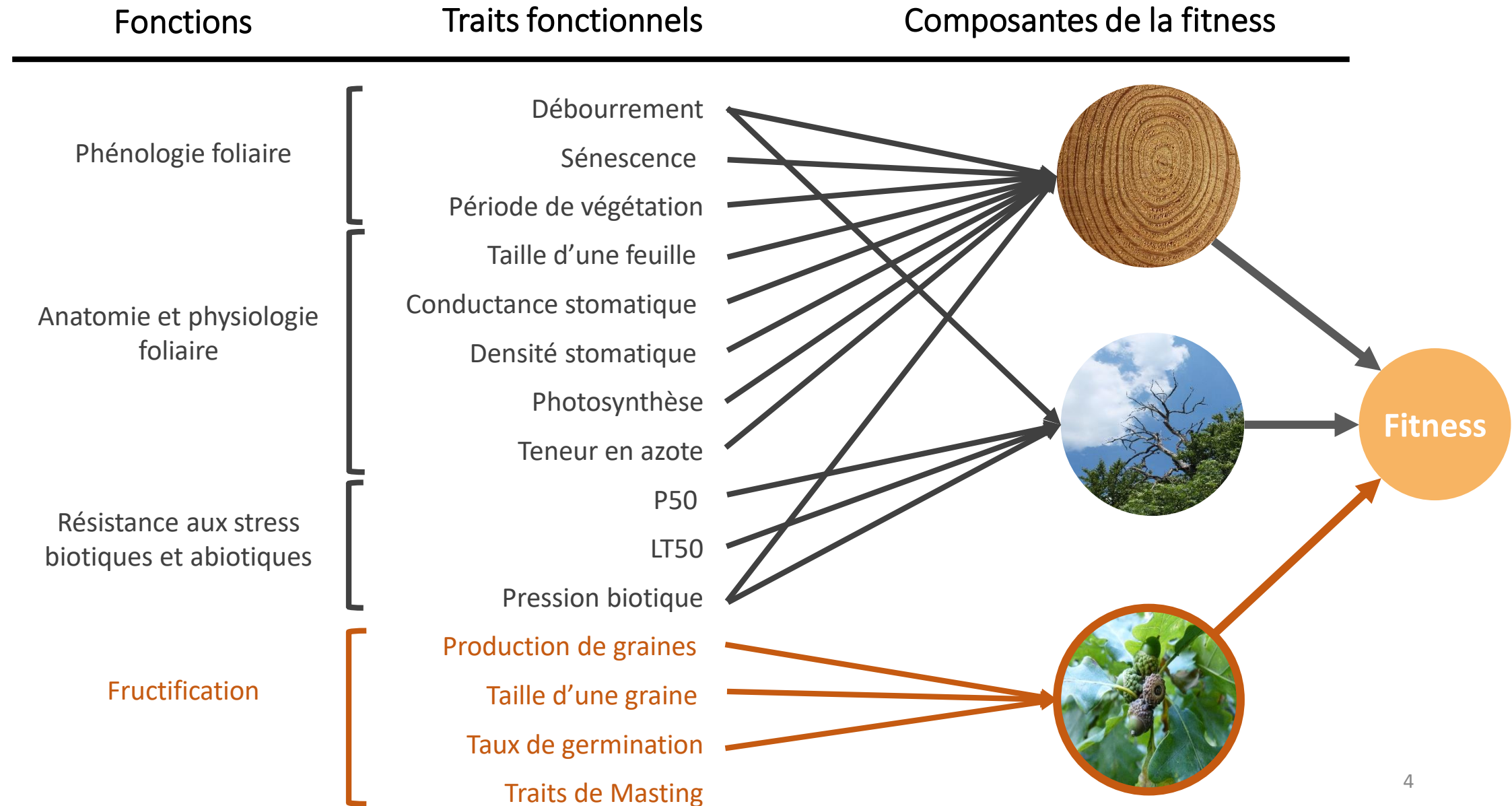
Traits d'histoire de vie des arbres



Traits d'histoire de vie et traits fonctionnels: schéma conceptuel



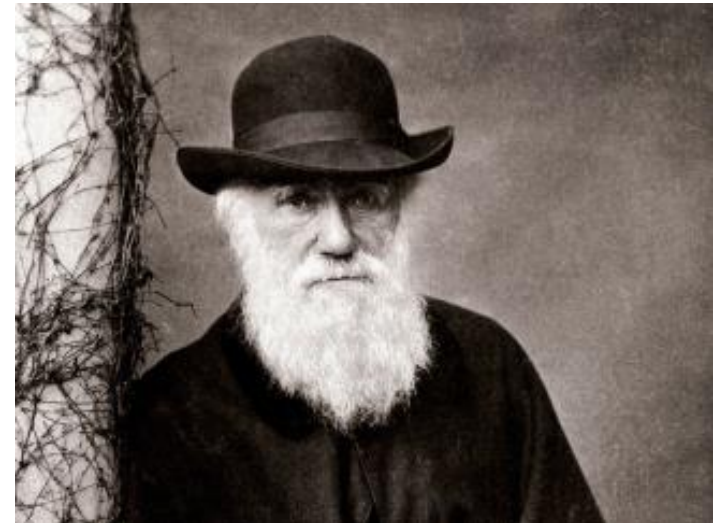
Traits d'histoire de vie et traits fonctionnels: schéma conceptuel



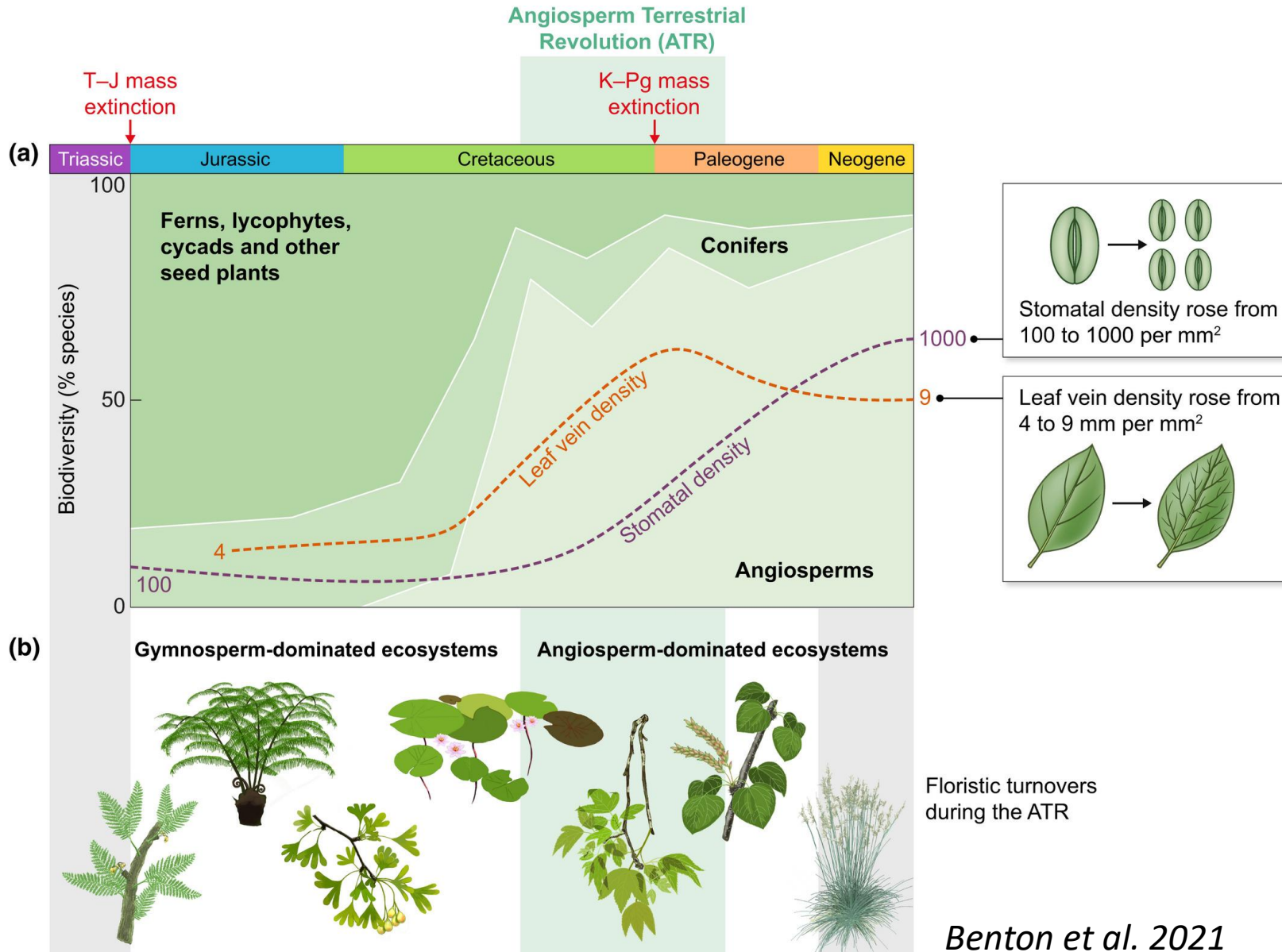
Darwin's abominable mystery

*“The rapid development as far as we can judge of all the higher plants within recent geological times is an **abominable mystery**”*

Lettre de correspondance entre C. Darwin et J. Hooker - 2 juillet 1879



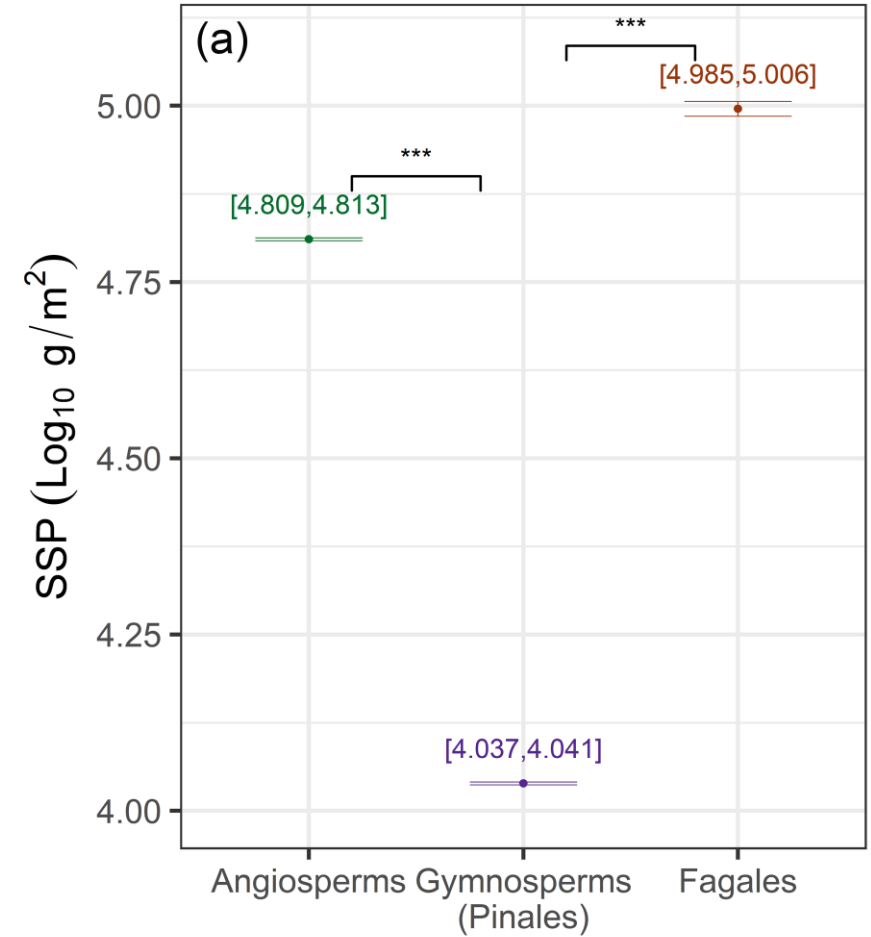
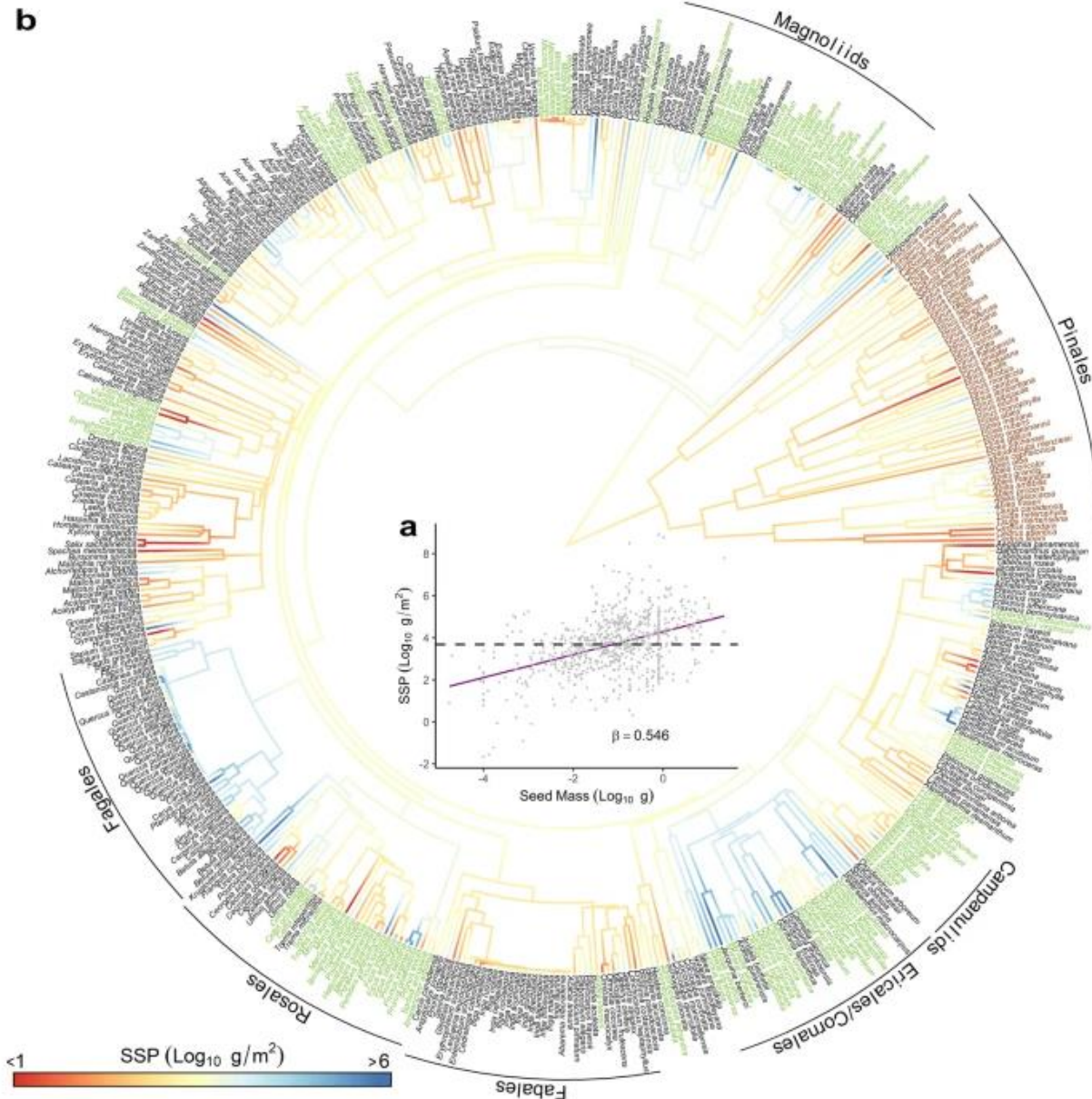
Comment les angiospermes ont-ils dominé le règne végétal



Aujourd'hui:

- 1 000 espèces de Gymnosperme
- 300 000 espèces d'Angiosperme

Darwin's abominable mystery



La reproduction des arbres forestiers: le Masting

12 Octobre 2021 – Oloron Sainte-Marie



© Thomas Caignard

La reproduction des arbres forestiers: le Masting

14 septembre 2022
Liverpool (GB)



© Andrew Hacket-Pain

12 Octobre 2021
Oloron Sainte-Marie



© Thomas Caignard

29 mai 2008
forêt domaniale de Trois Fontaines



© François Debias

La reproduction des arbres forestiers: le Masting



© Andrew Hackett-Pain

Hêtre commun – *Fagus sylvatica*



© Betsey Crawford

Epinette blanche – *Picea glauca*

La reproduction des arbres forestiers: le Masting



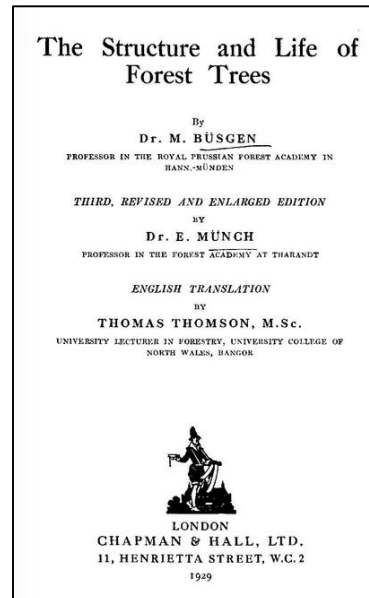
La reproduction des arbres forestiers: le Masting



Les Très Riches Heures du duc de Berry, France
– Frères Limbourg (1416)



Psautier de la reine Marie, Grande Bretagne
- (1310-1320)

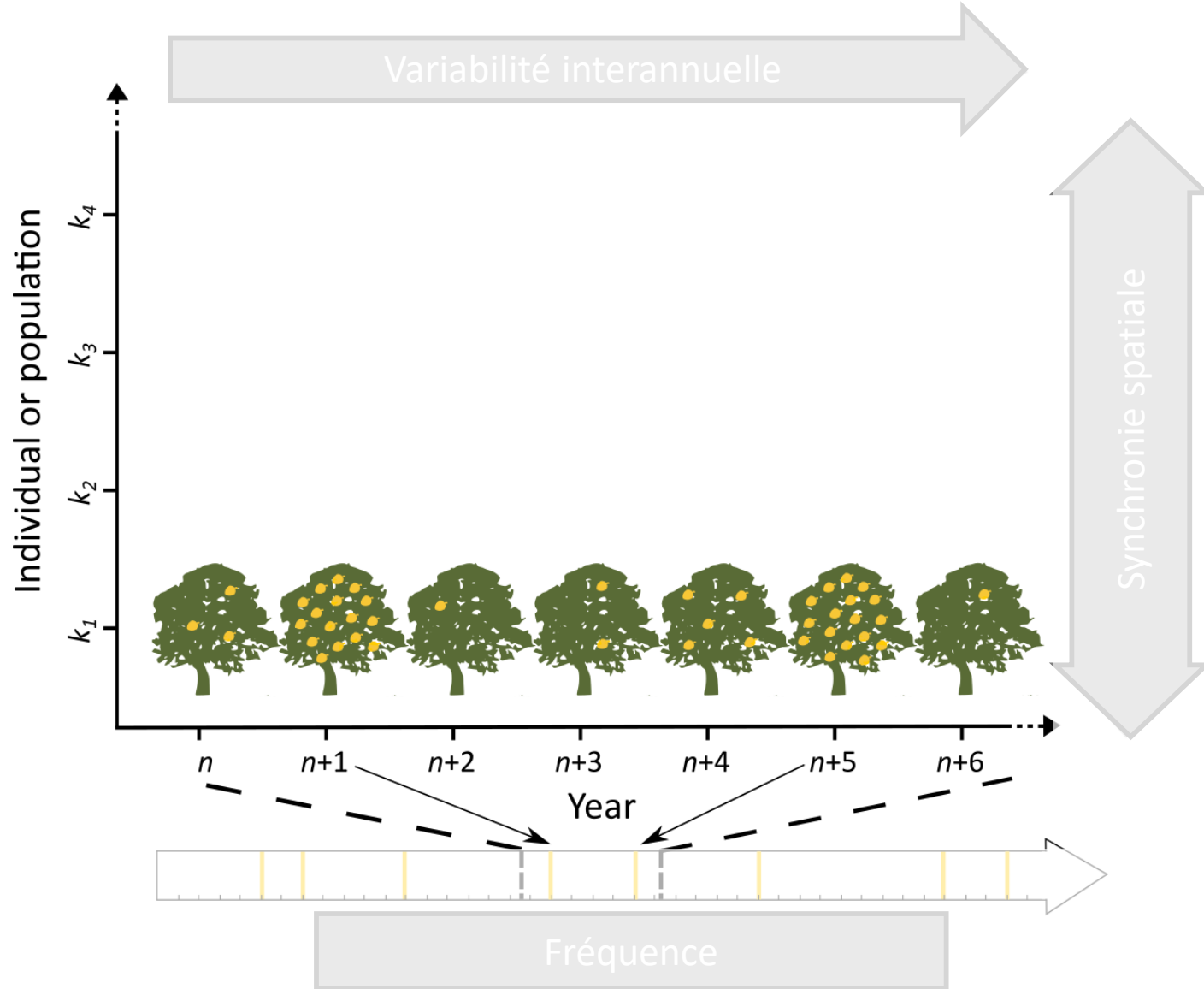


Büsgen & Münch –
The structure and life of forest trees
(1929)

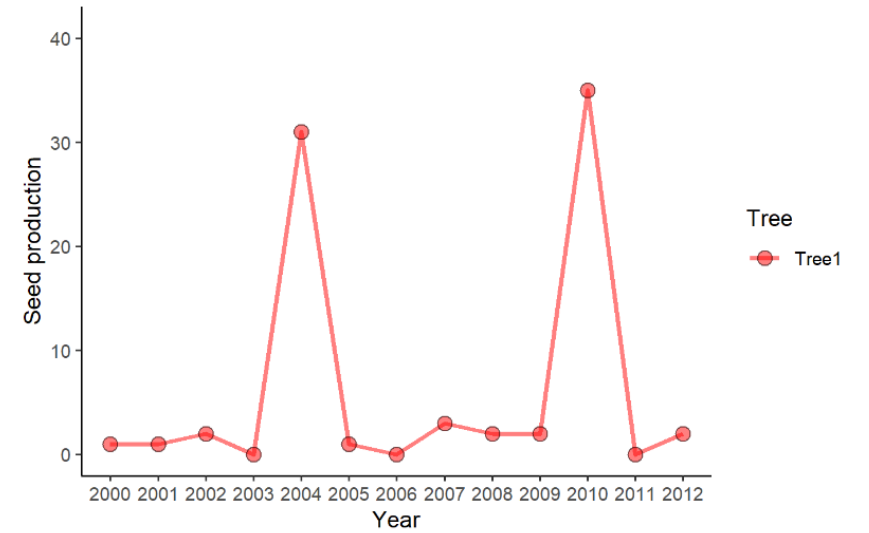
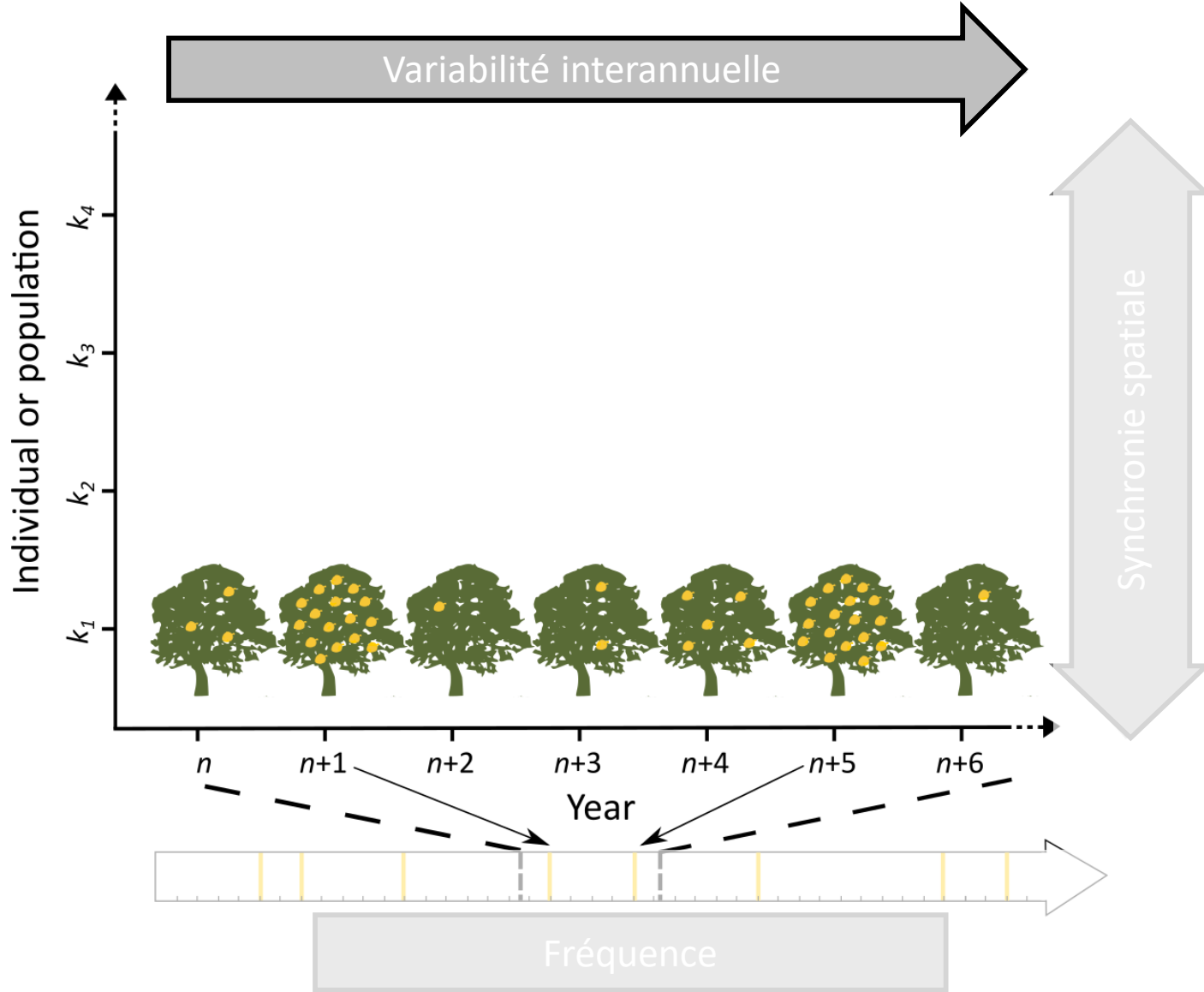
- Production fructifère massive à l'échelle d'une population:
 - Fortes variabilités interannuelles
 - Absence de périodicité
 - Synchronie
 - Autocorrélation temporelle négative (lag1)

 **Phénomène de Masting**

Phénomène de masting



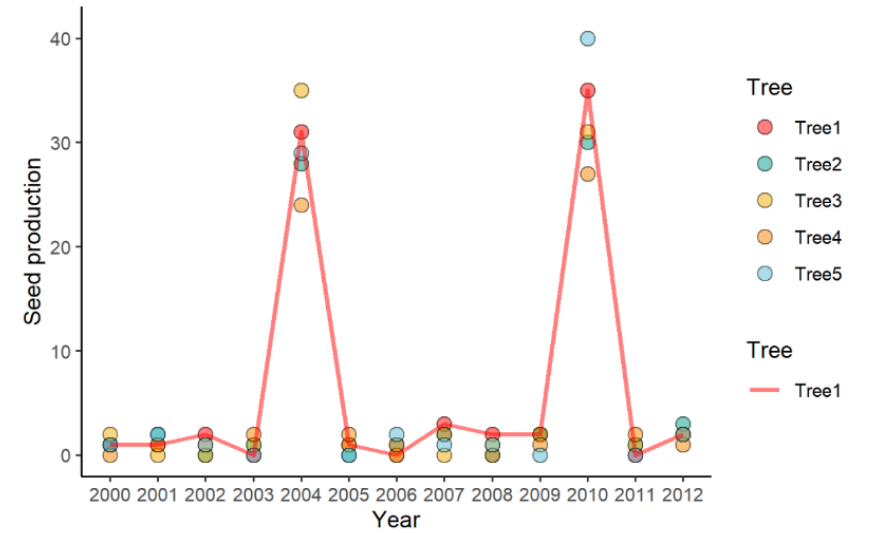
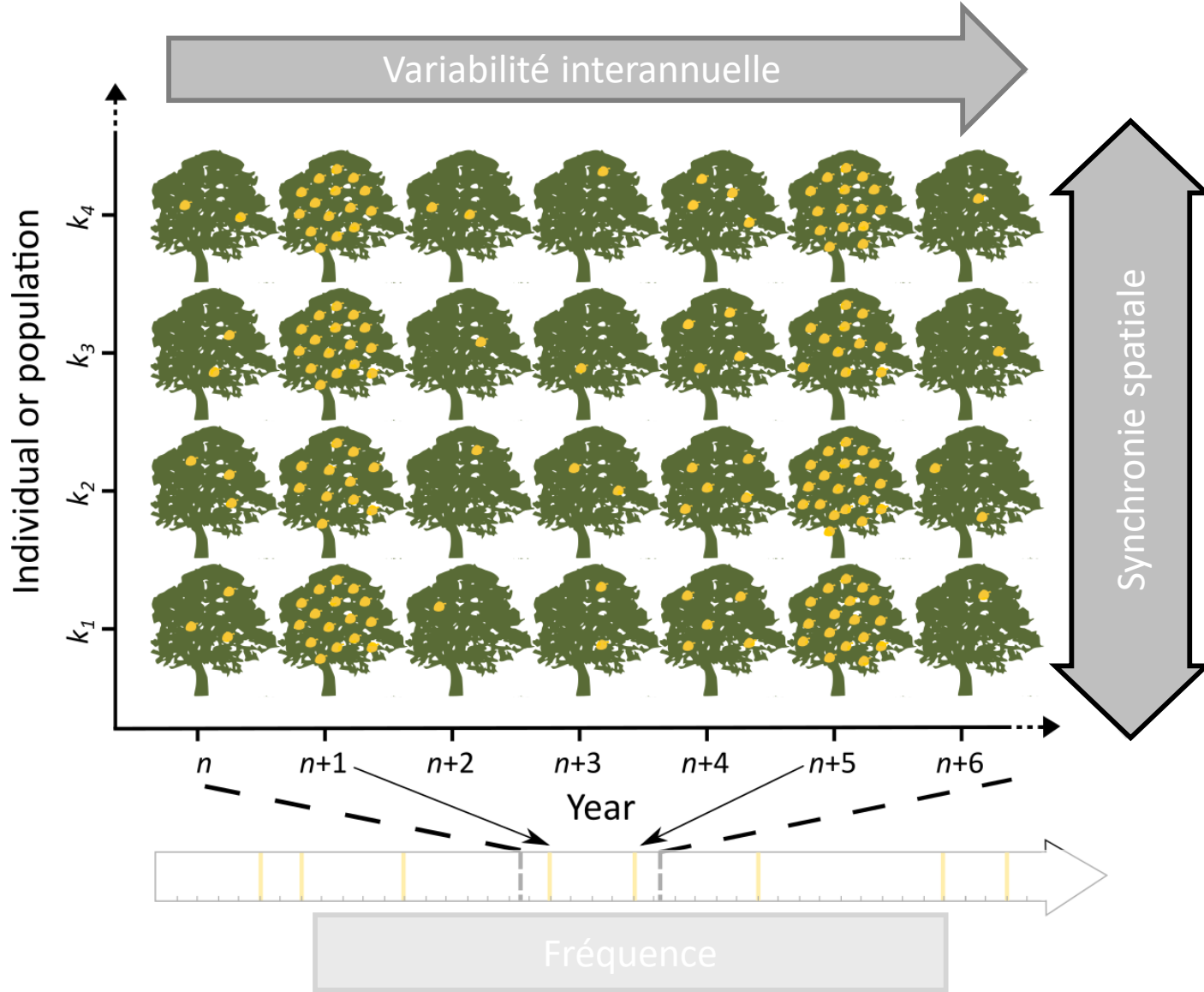
Phénomène de masting



Coefficient de variation à l'échelle de l'individu:

$$CV_i = \frac{\sigma}{\mu}$$

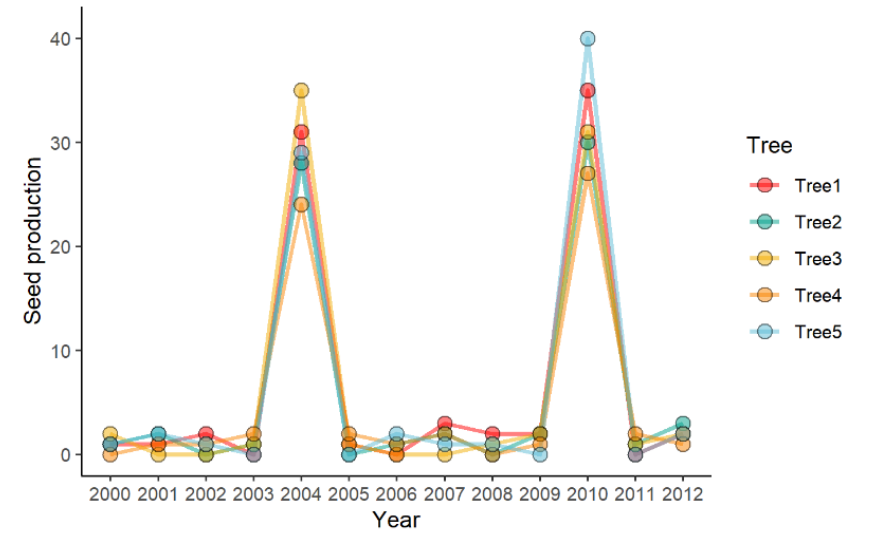
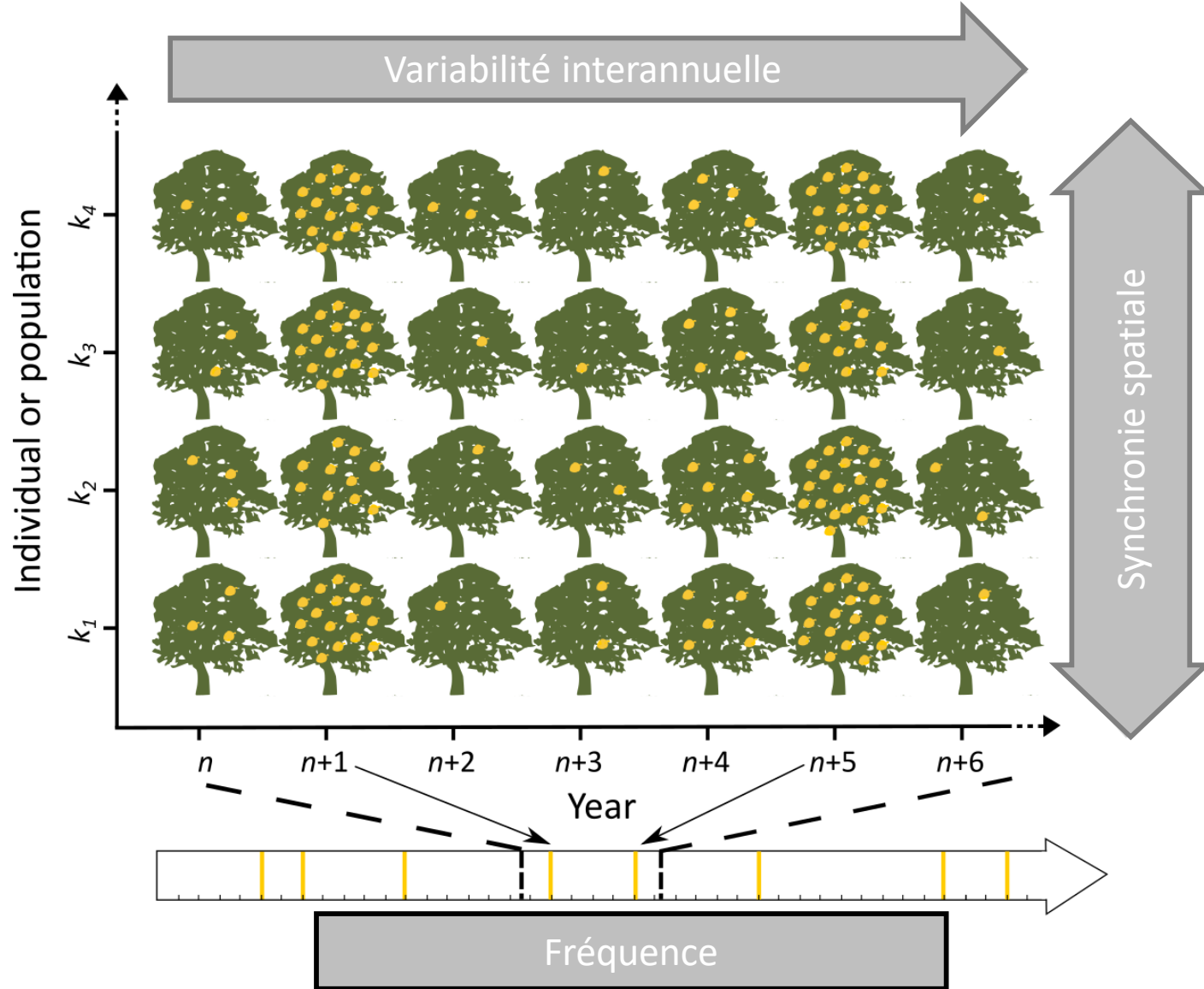
Phénomène de masting



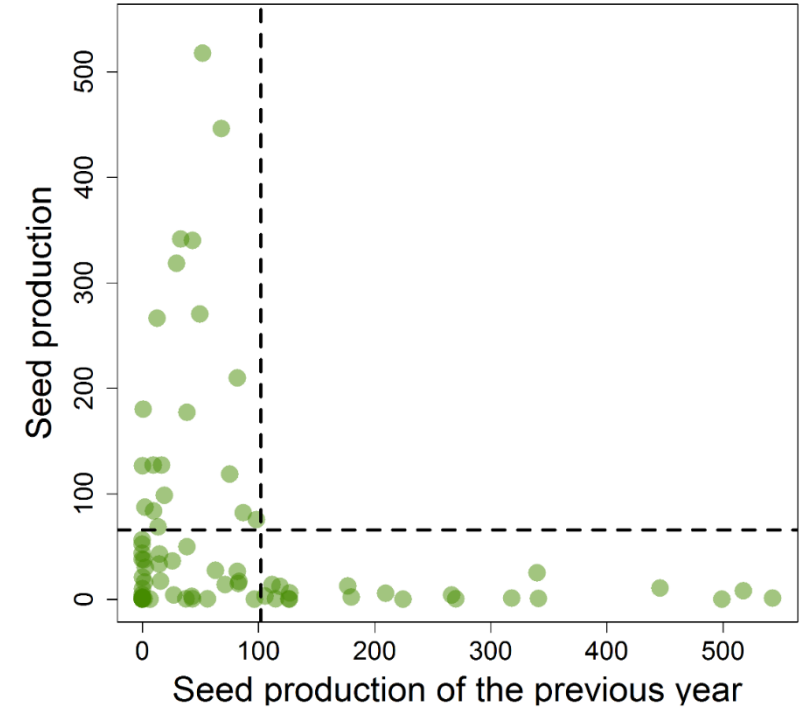
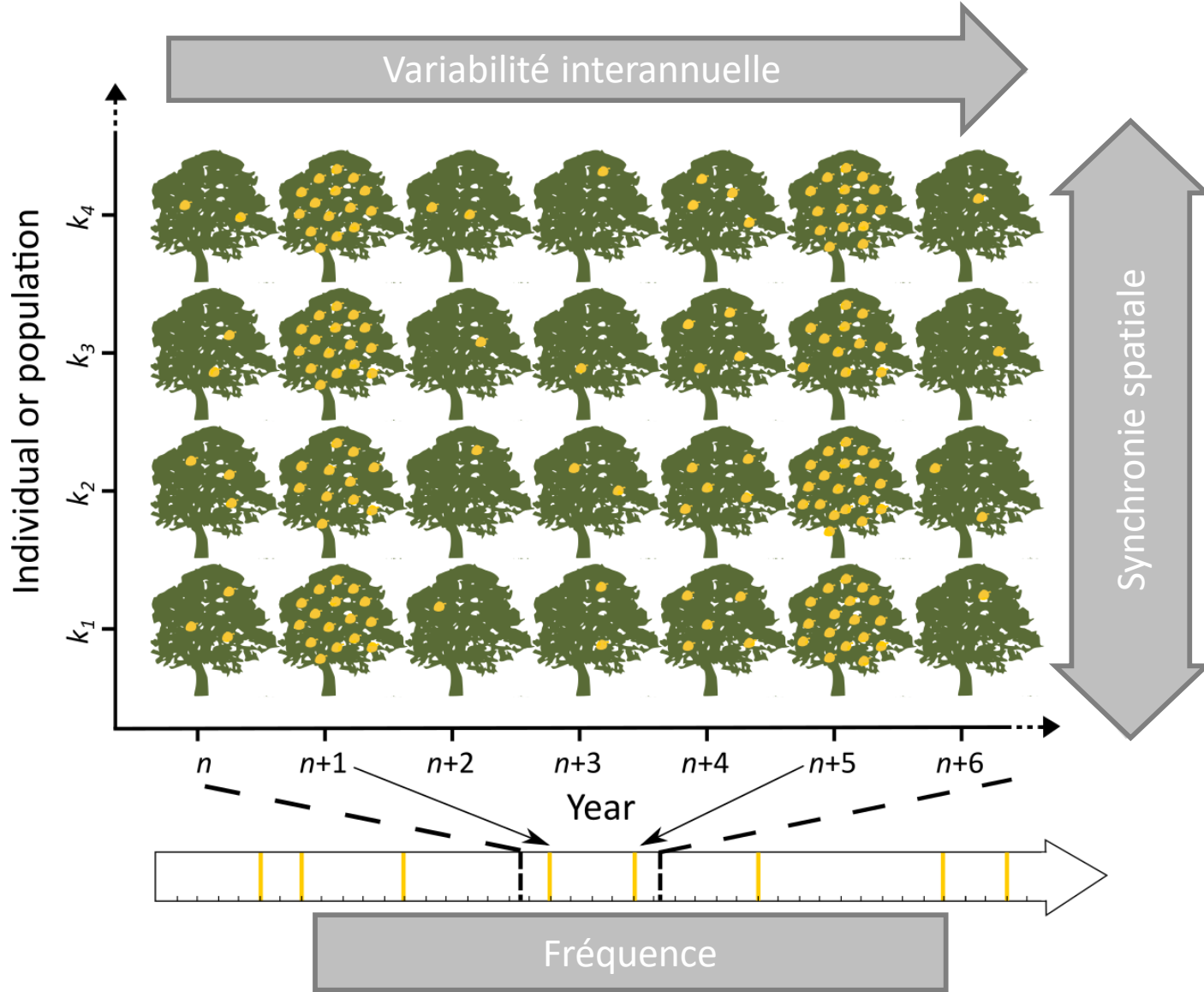
Coefficient de corrélation de Spearman:

$$S_i = \frac{6 \sum d_i^2}{n(n^2 - 1)}$$

Phénomène de masting



Phénomène de masting



Autocorrélation temporelle:

$$\gamma_k = E((X_t - \mu)(X_{t+k} - \mu))$$

$$\rho_k = \frac{\gamma_k}{\sigma^2}$$

Phénomène de masting

- Espèce dominante dans son milieu.
- Pollinisation par le vent: Anémogamie
- Espèce monoïque
- Pollinisation croisée



Quercus douglasii



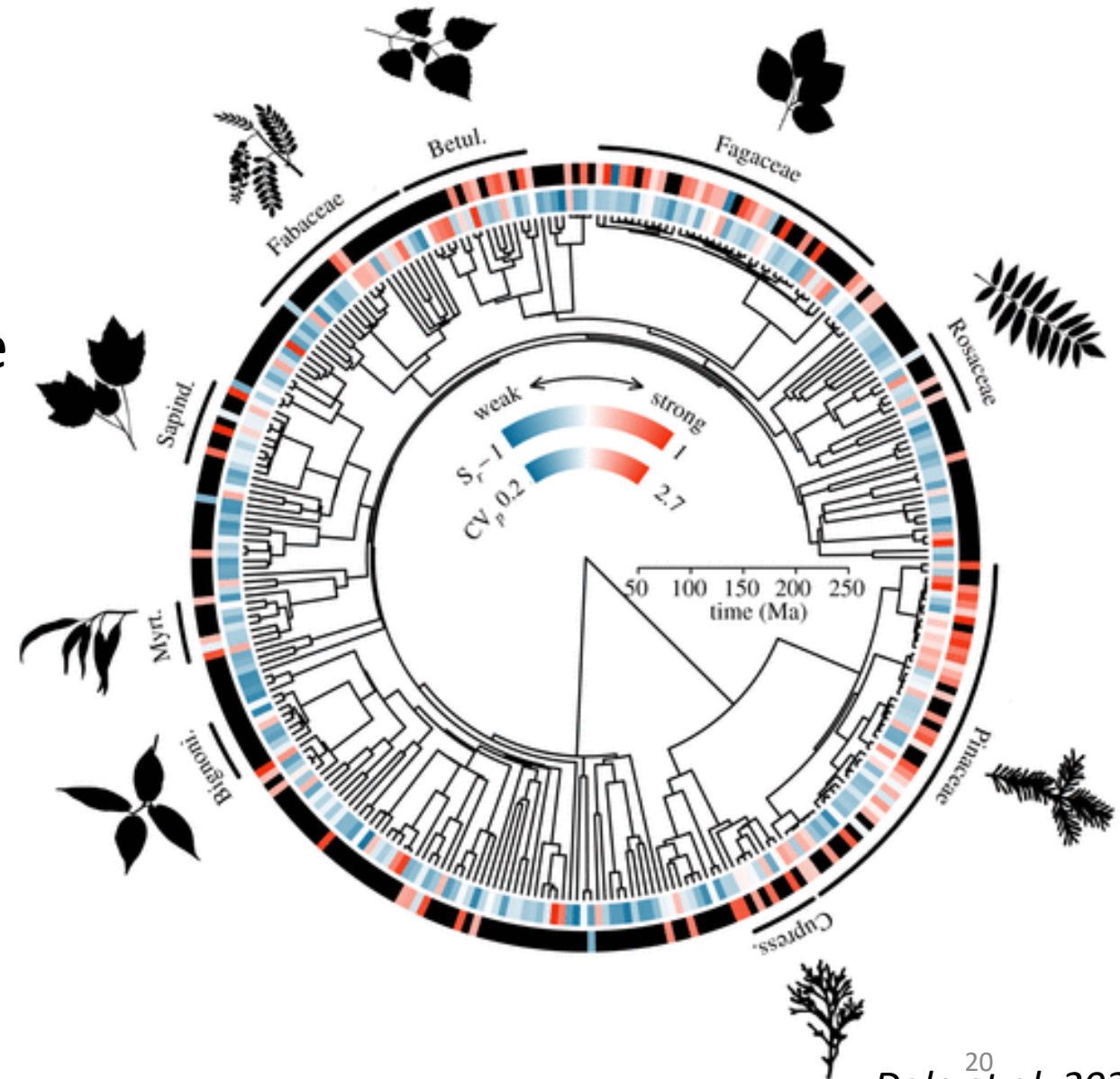
Pinus albicaulis



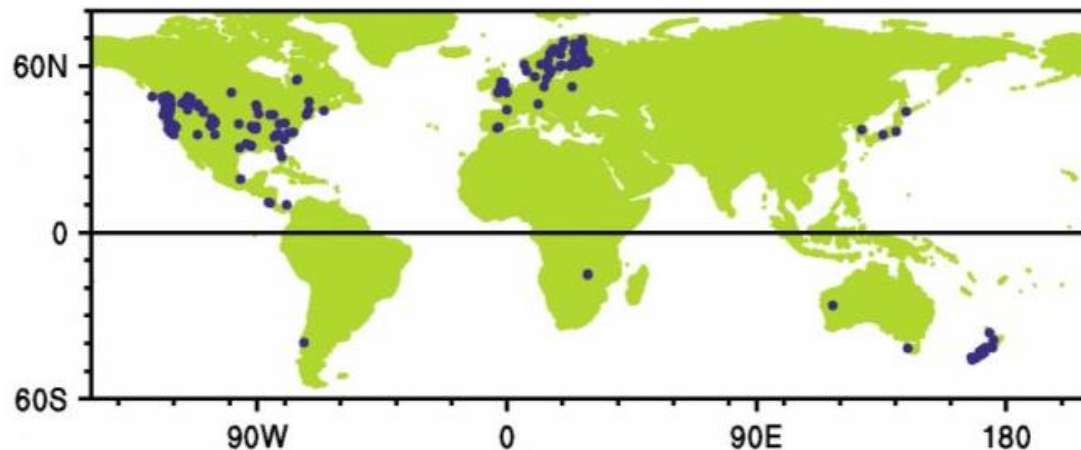
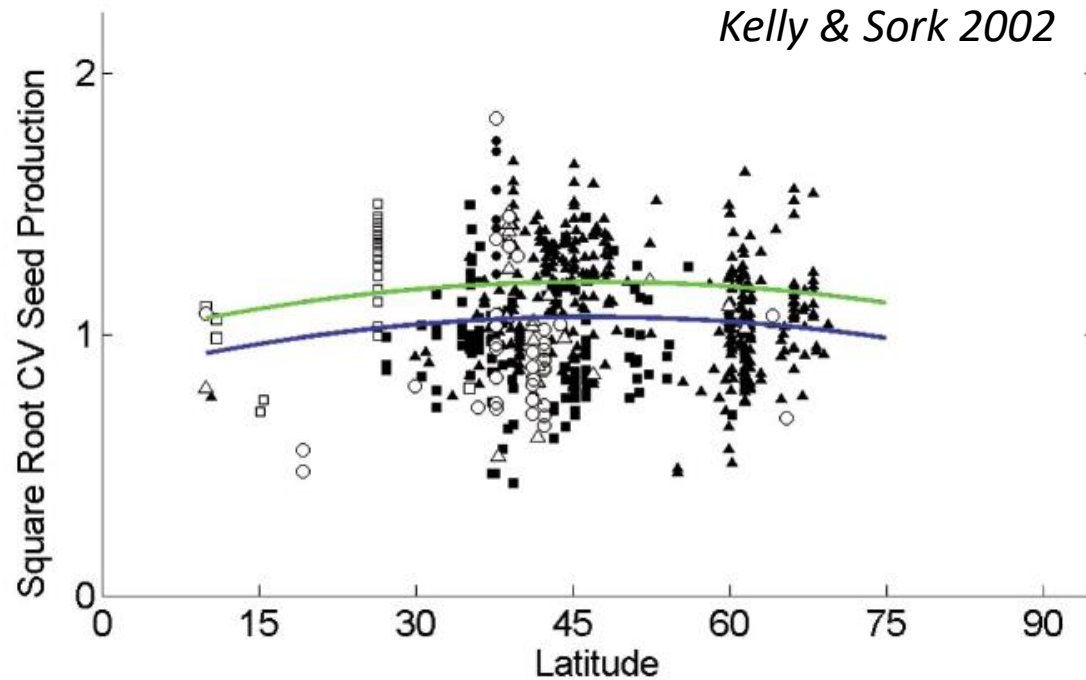
Chionochloa flavicans

Phénomène de masting

- Espèce dominante dans son milieu.
- Pollinisation par le vent: Anémogamie
- Espèce monoïque
- Pollinisation croisée



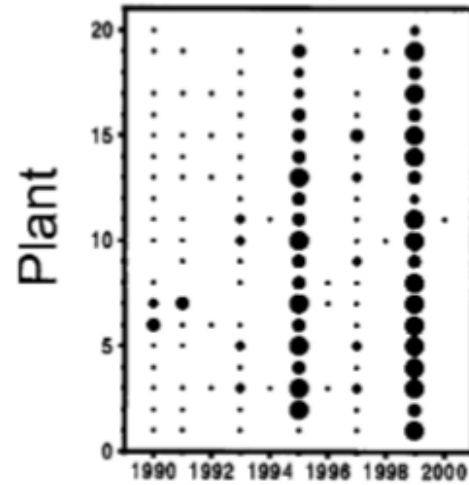
Variabilité interspécifique du masting



- On retrouve des espèces de masting dans la plupart des écosystèmes terrestres
- L'intensité du masting est différente entre les espèces.

Variabilité interspécifique du masting

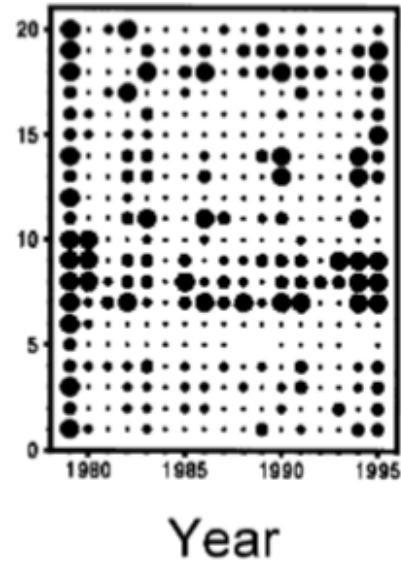
Chionochloa pallens



- **Forte** variabilité temporelle (CV_i)
- **Forte** Synchronie (r)



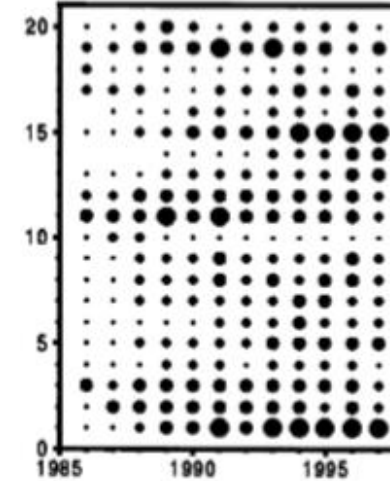
Elaeocarpus dentatus



- **Faible** variabilité temporelle (CV_i)
- **Faible** Synchronie (r)



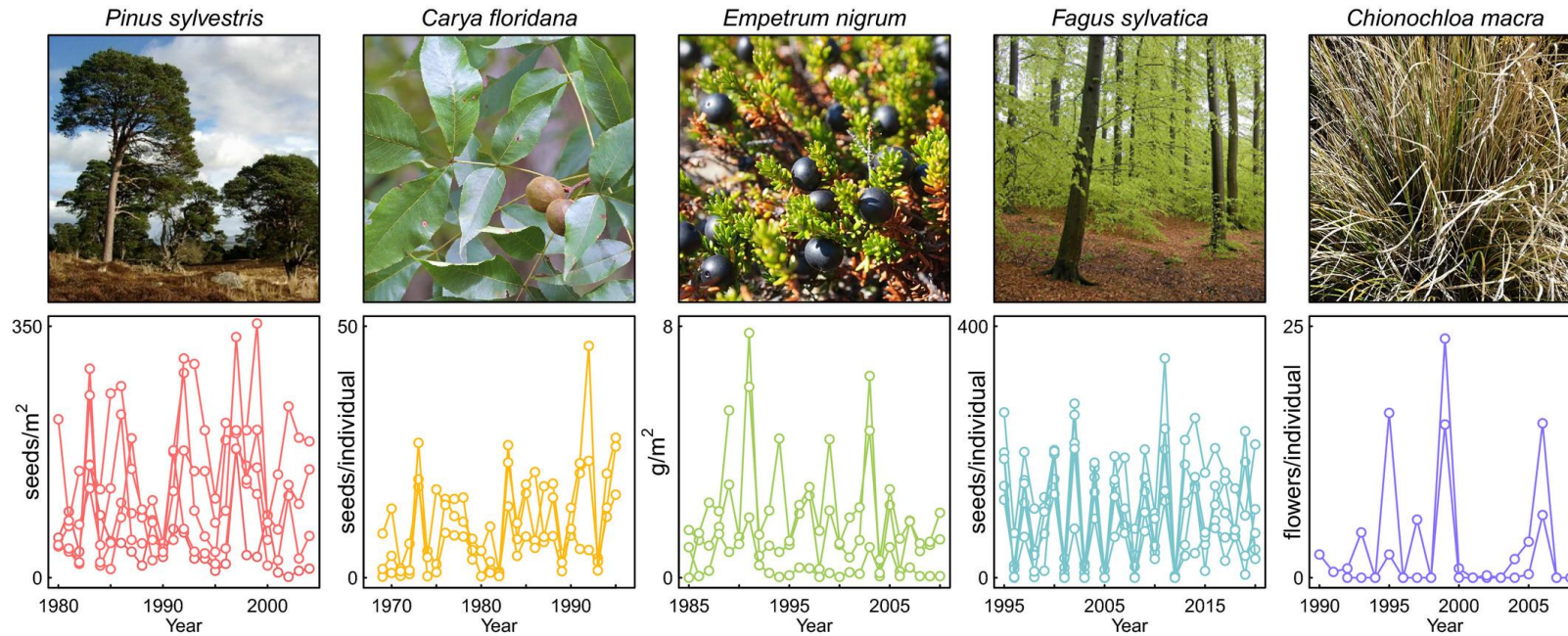
Lavendula latifolia



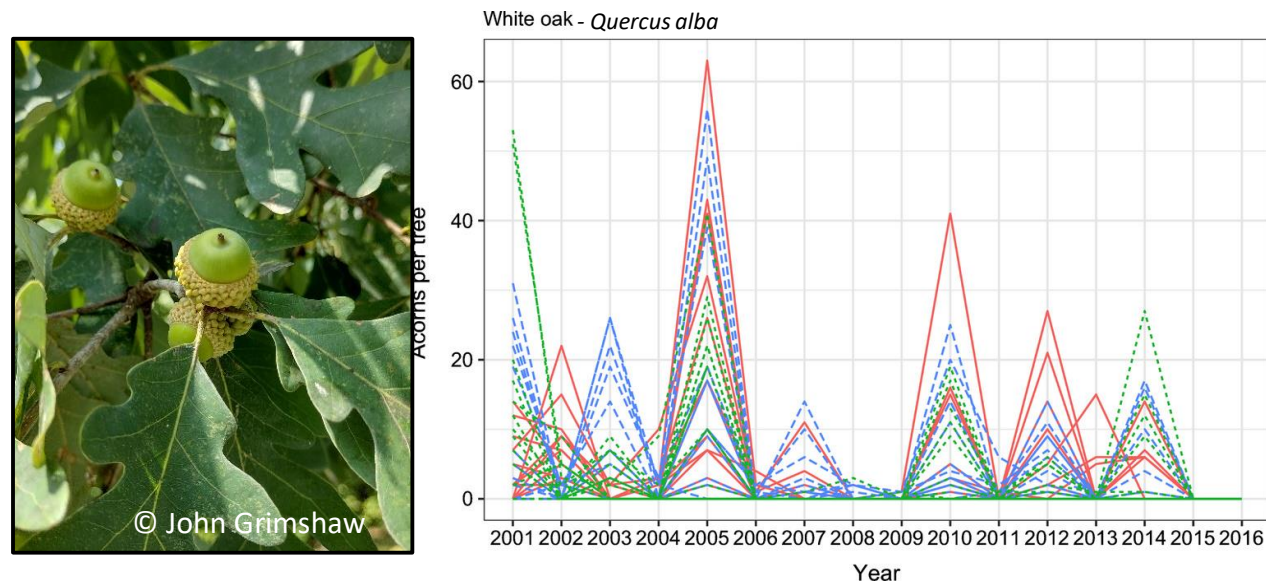
- **Très faible** variabilité temporelle (CV_i)
- Synchronie **modérée** (r)



Variabilité interspécifique du masting



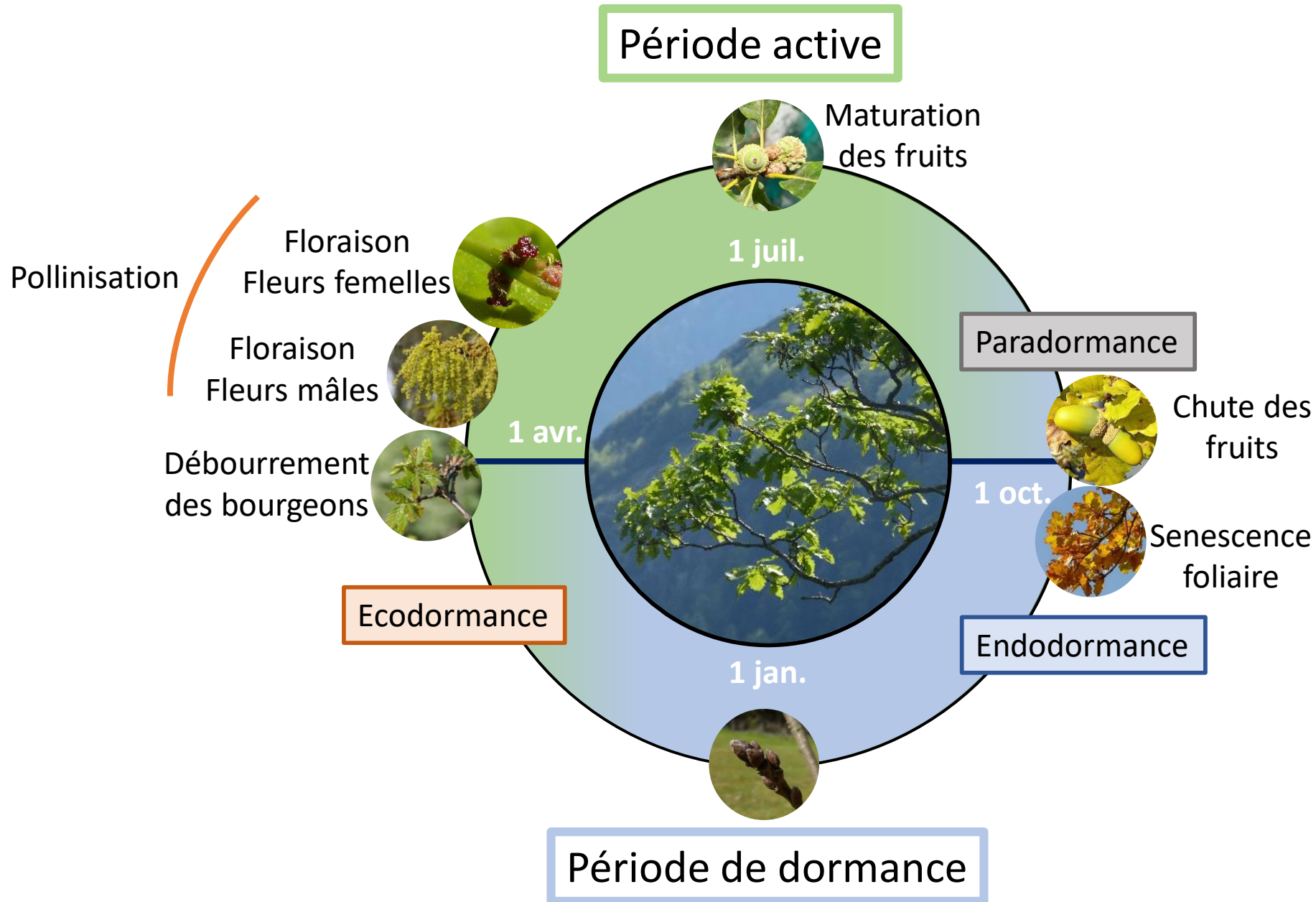
Hacket-Pain et al. 2022



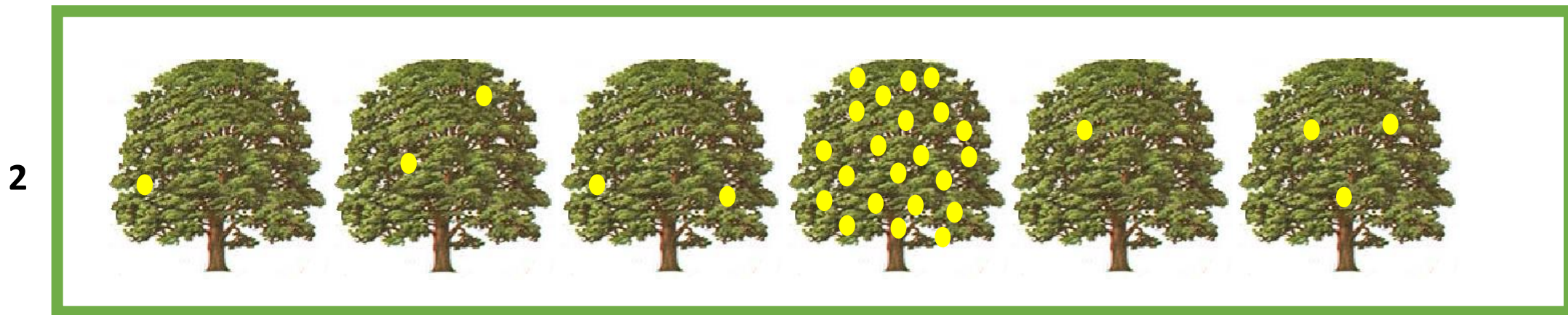
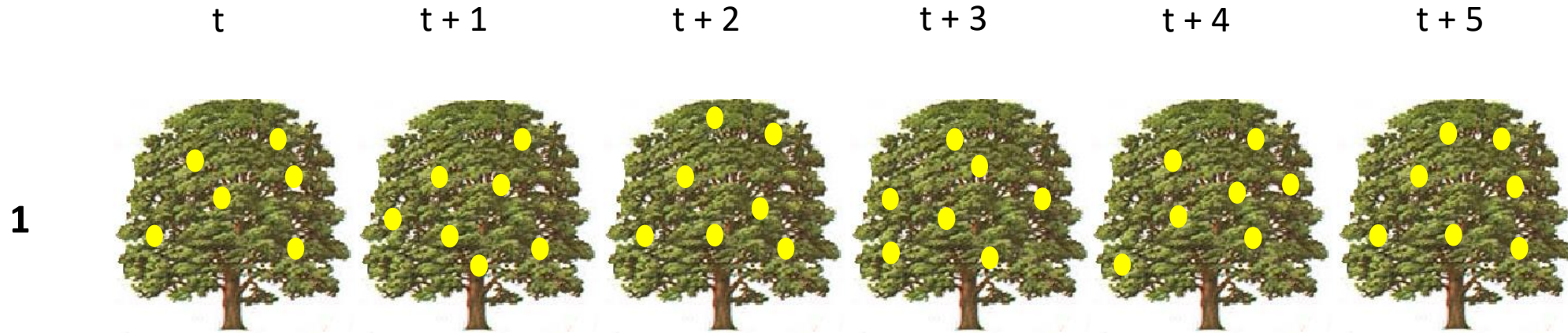
© John Grimshaw

Bogdziewicz et al. 2018

Phénologie de la reproduction du chêne



Causes Ultimes: Un avantage évolutif



Avantage évolutif

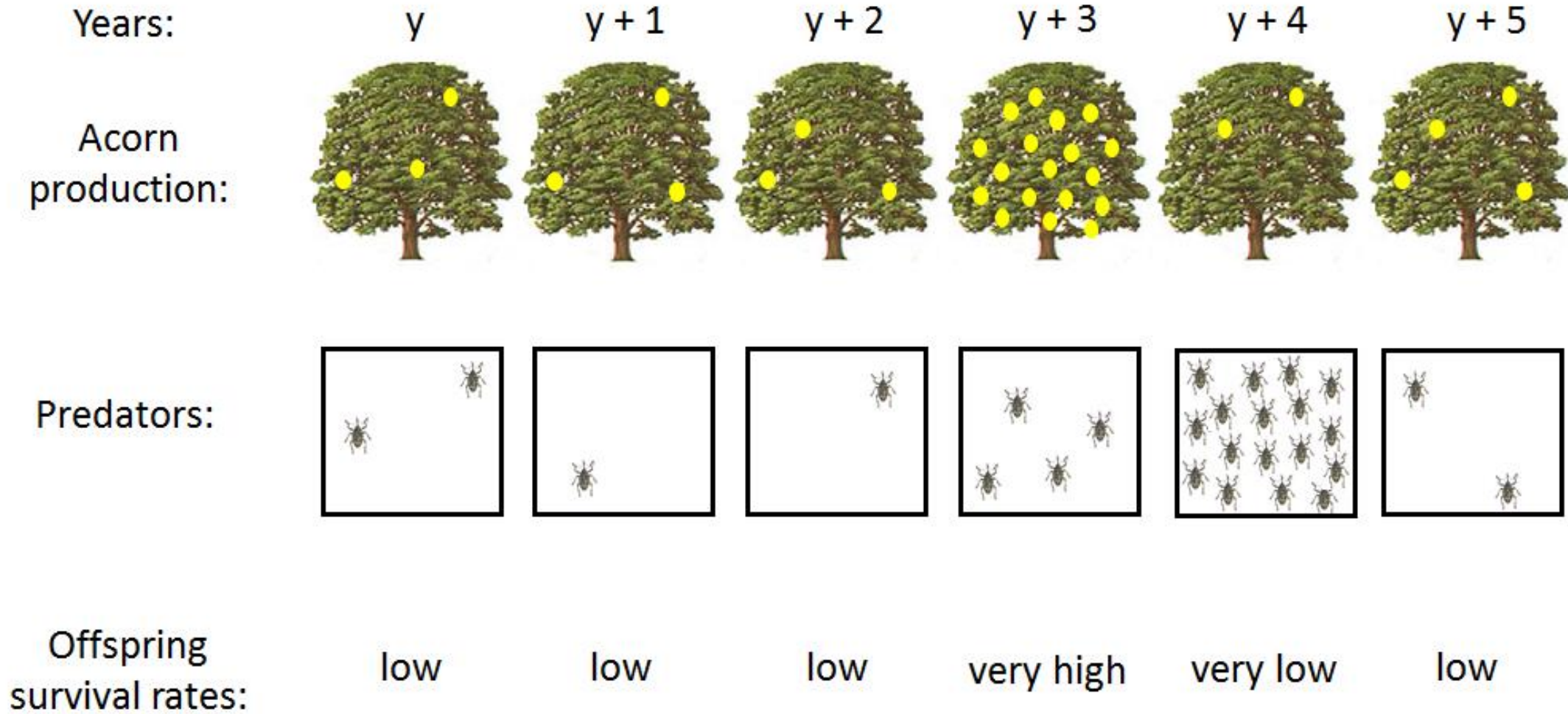


Economie d'échelle - « Economy of scale »
(Janzen 1978)

Causes Ultimes: « predator satiation »



Curculio glandium



Causes Ultimes: « predator satiation »



Curculio glandium

Michael Whitlock a retweeté



Stephen Heard
@StephenBHeard

If you've ever worried that you look silly doing something: first, why worry about that? And second, consider this weevil.

[Traduire le Tweet](#)



Adrian Smith @DrAdrianSmith · 14 sept.

Bless your heart, weevil (Curculio sp.)

bless your goofy little heart



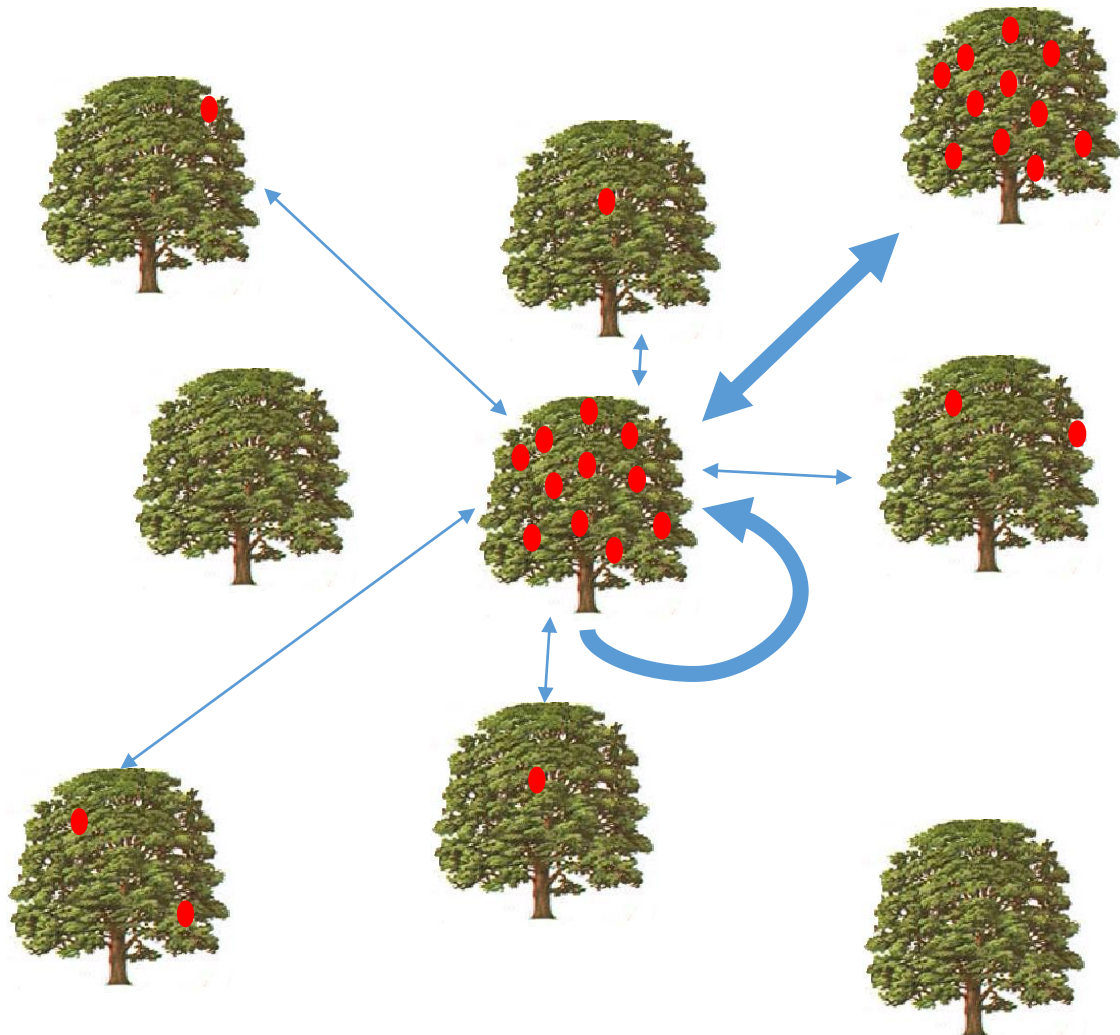
6:20 PM · 14 sept. 2020 · Twitter Web App

17 Retweets 2 Tweets cités 57 J'aime

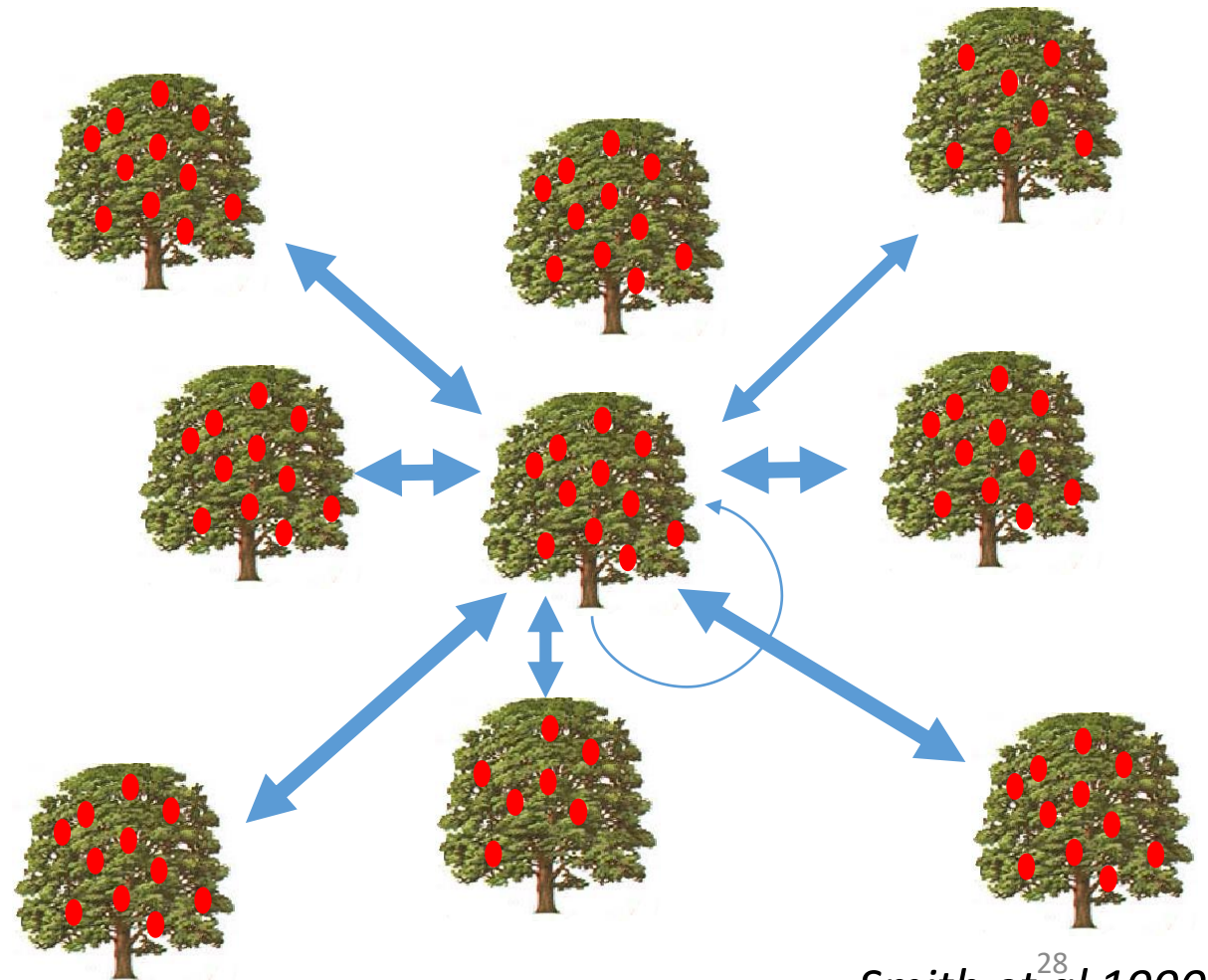


Causes Ultimes: « Pollination efficiency »

Non Mast Year



Mast Year



Causes Ultimes: « Animal dispersal »



Ecureuil roux - *Tamiasciurus hudsonicus*



Cône d'Épinette blanche – *Picea glauca*

Causes Ultimes: « Animal dispersal »



Mulot sylvestre
Apodemus sylvaticus



Geai des chênes
Garrulus glandarius

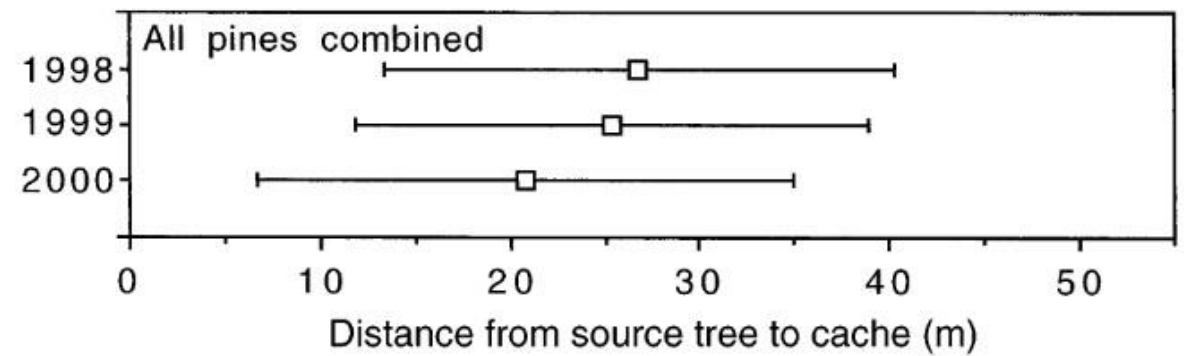
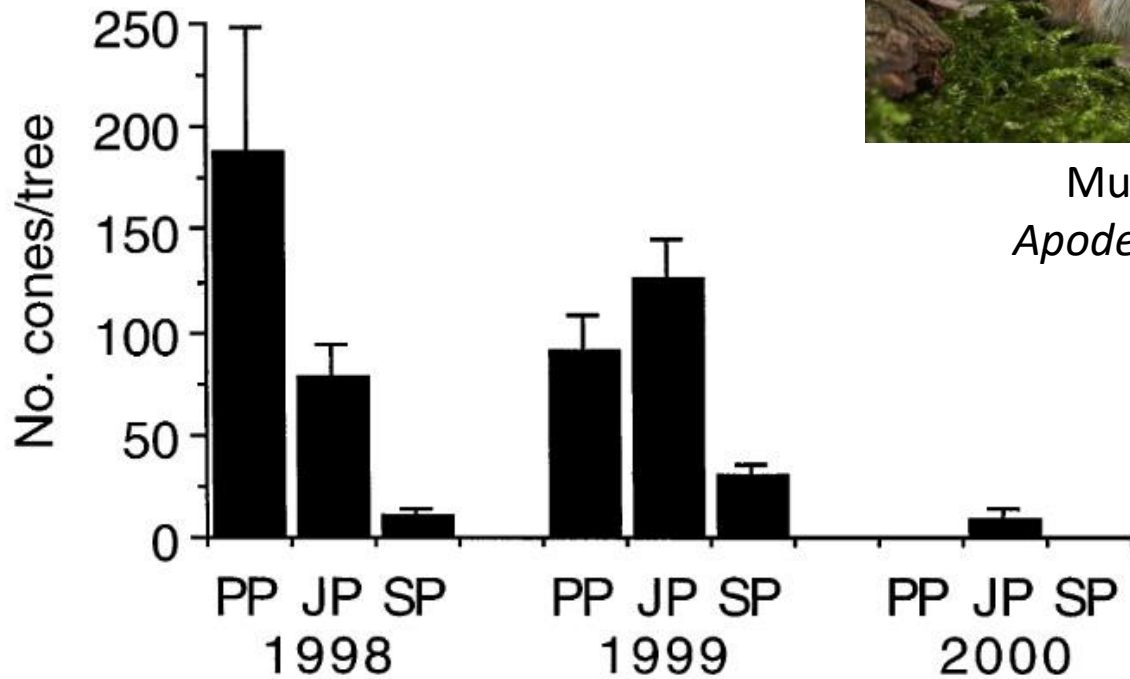
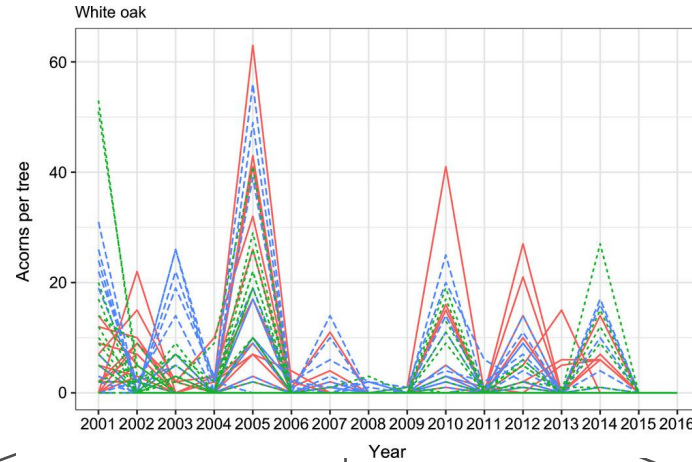


FIG. 1. Cone crops (mean + 1 SE) of ponderosa pine (PP), Jeffrey pine (JP), and sugar pine (SP) from 1998 to 2000. $N = 28-30$ mature trees for each species and year.

Causes Ultimes: une économie d'échelle



Economie d'échelle

Régénération forestière

© François Debias

Brassage génétique

© Thomas Caignard

Dispersion des graines

© Phil Winter

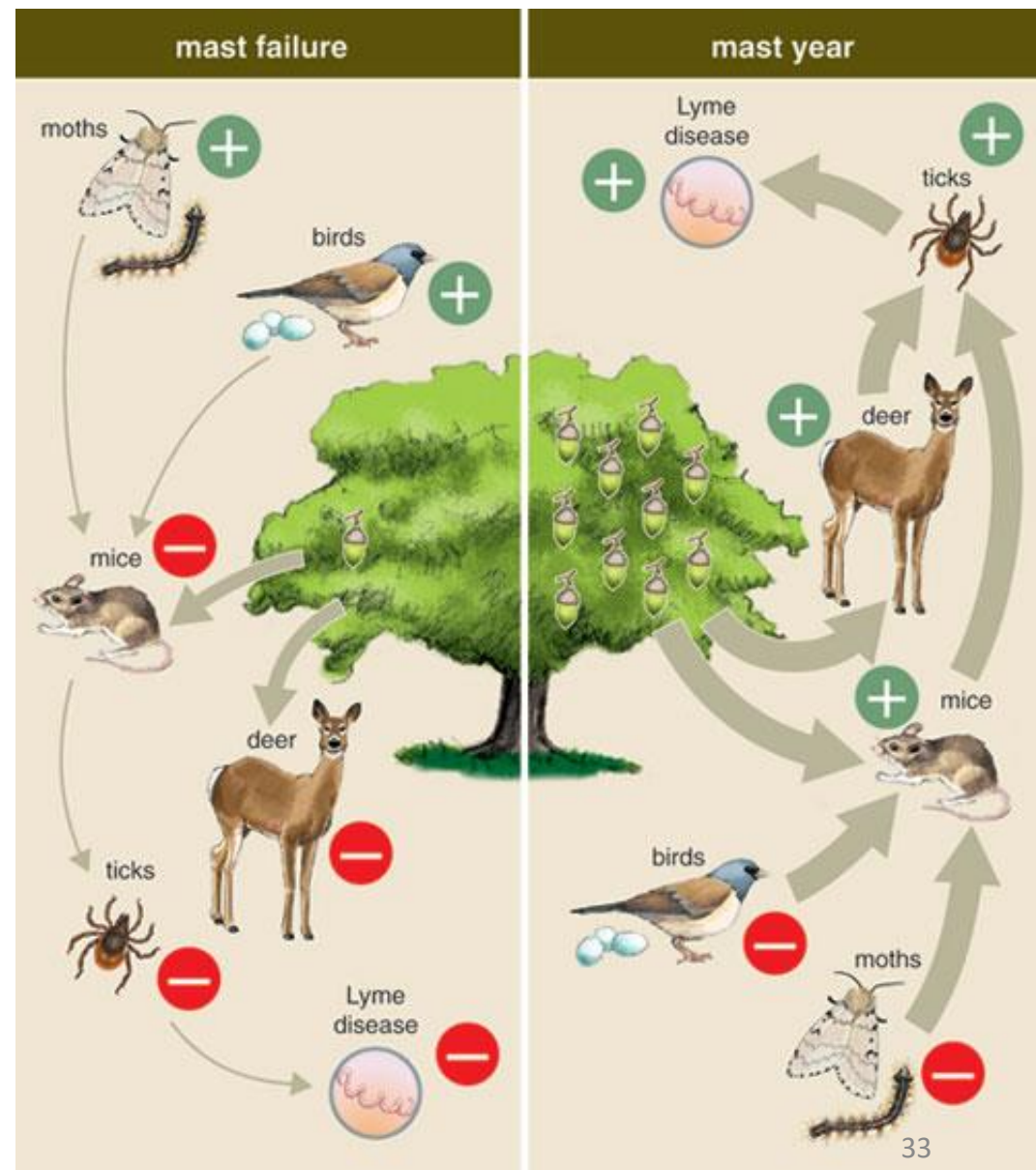
Concept **d'économie d'échelle**

- ⇒ L'avantage pour l'arbre est d'économiser son énergie qu'il concentre pour la reproduction.
- ⇒ Un fort investissement (forte production fruitière) est plus efficace en termes de survie pour la descendance que des petites productions réparties sur plusieurs années.

Impact du masting sur les écosystèmes

Effet du masting sur les réseaux trophiques:

- Generalist consumers
- Generalist predators
- Alternate prey
- Competitors
- Parasites & pathogens



Ostefeld & Keesing 2000
Koenig & Knops 2005

Impact du masting sur les écosystèmes

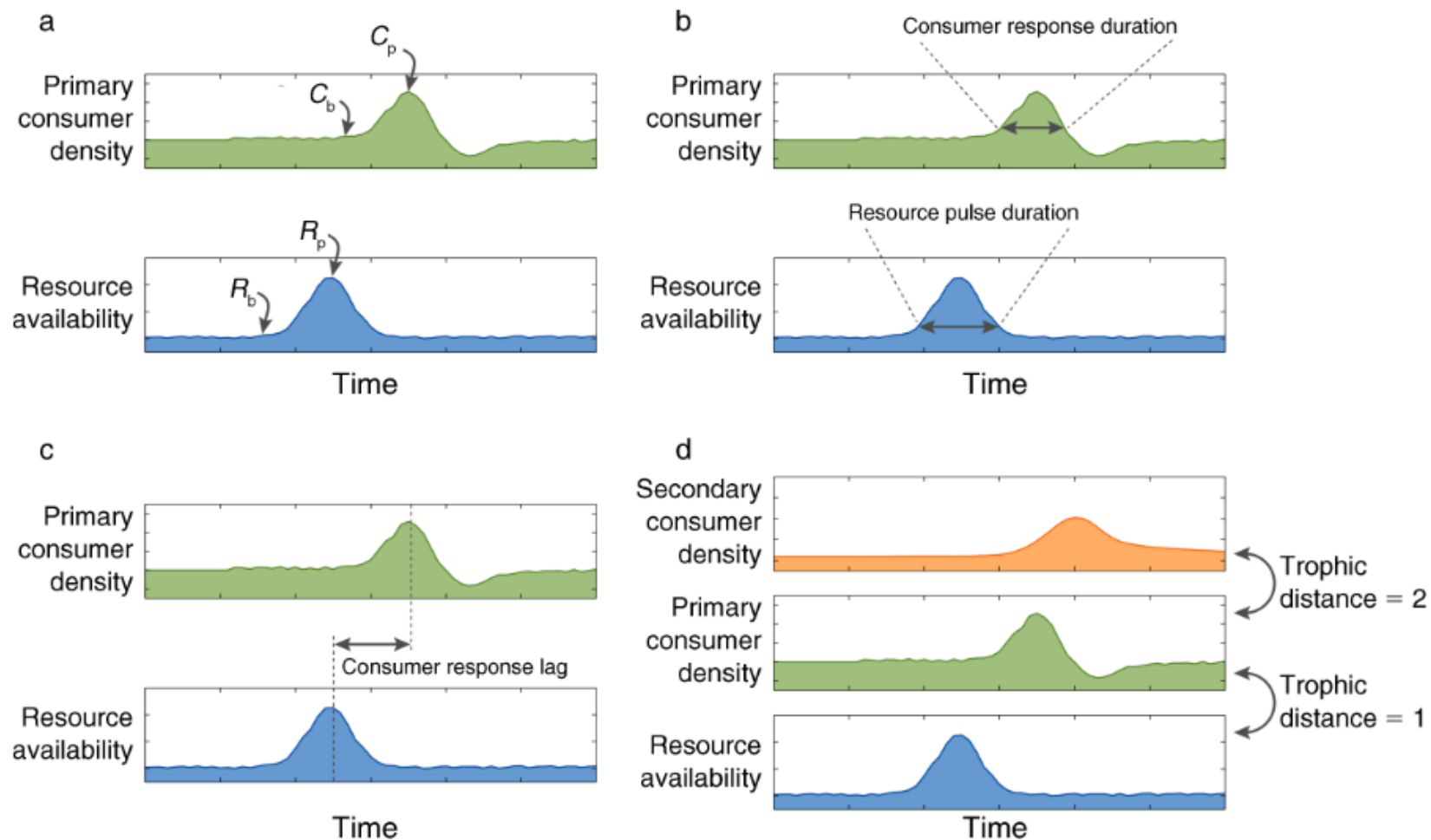
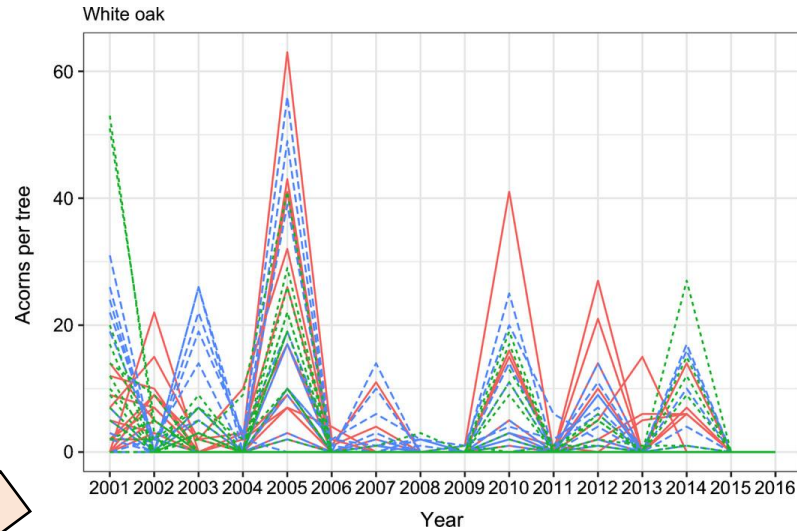
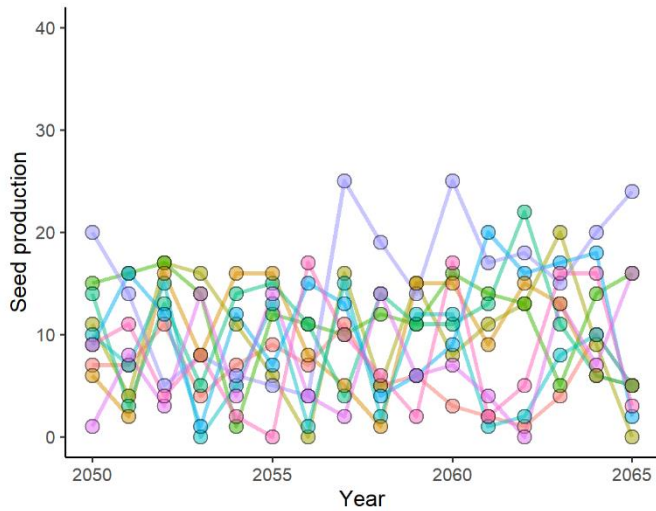


FIG. 1. A schematic diagram of extracted data used to investigate (a) resource pulse (R_p) and consumer response (C_p) magnitude relative to baselines (R_b and C_b), (b) resource pulse and consumer response duration, (c) the consumer response lag, and (d) indirect effects and trophic distance.

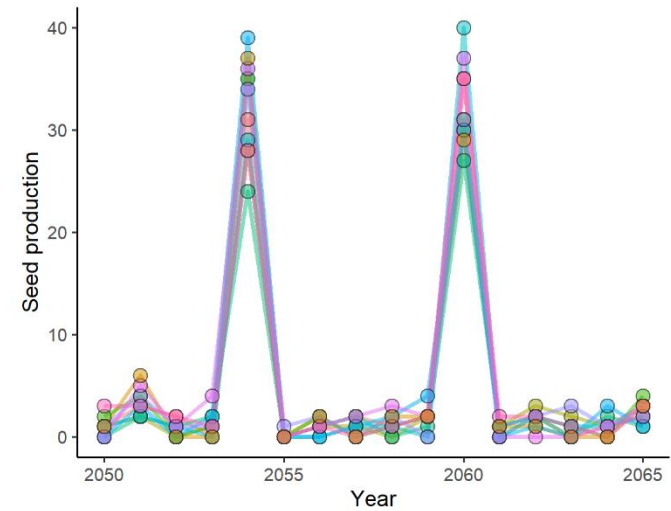
Impact du changement climatique sur la reproduction

Vers des fructifications régulières ?



Bogdziewicz
et al. 2018

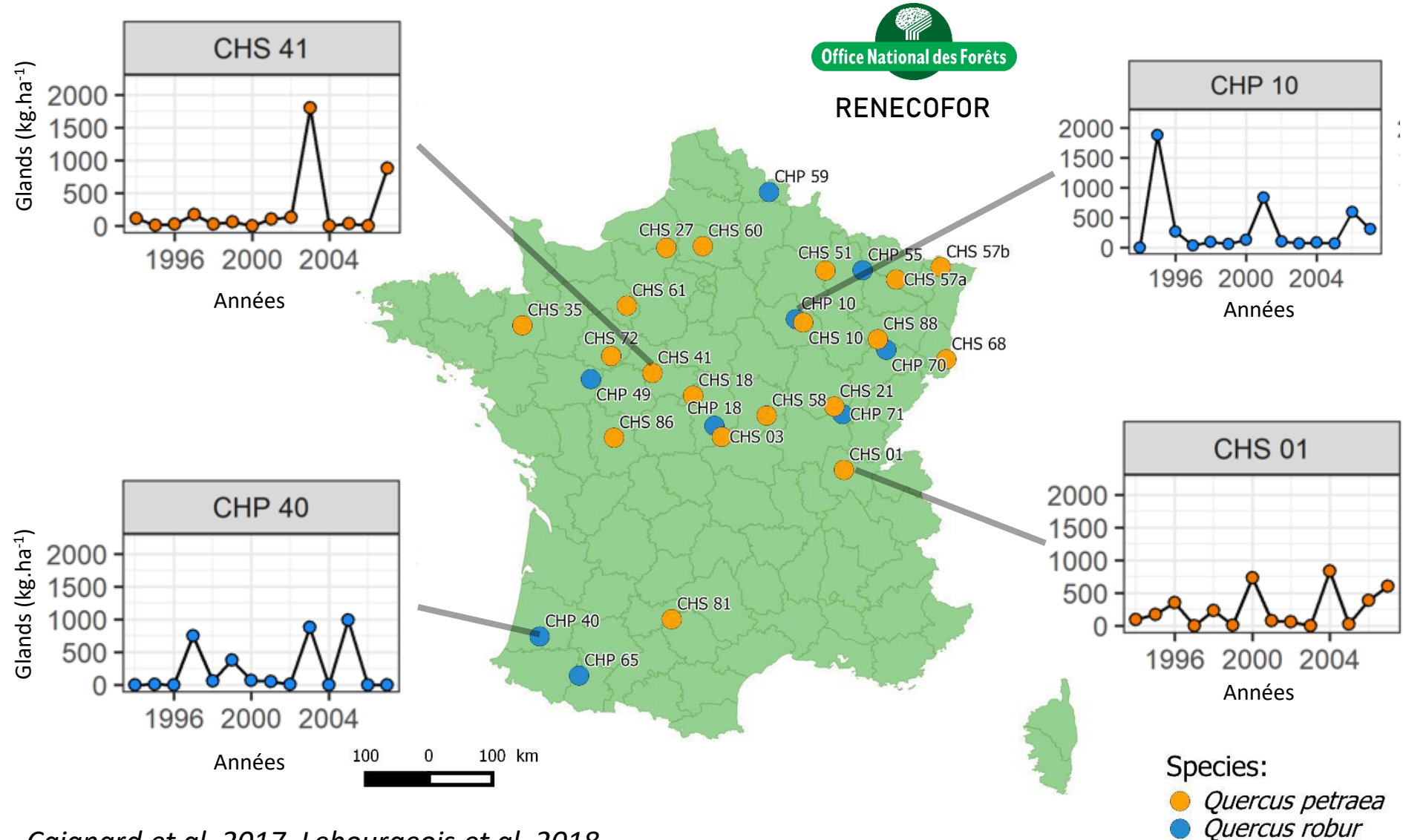
Vers des fructifications massives et plus rares ?



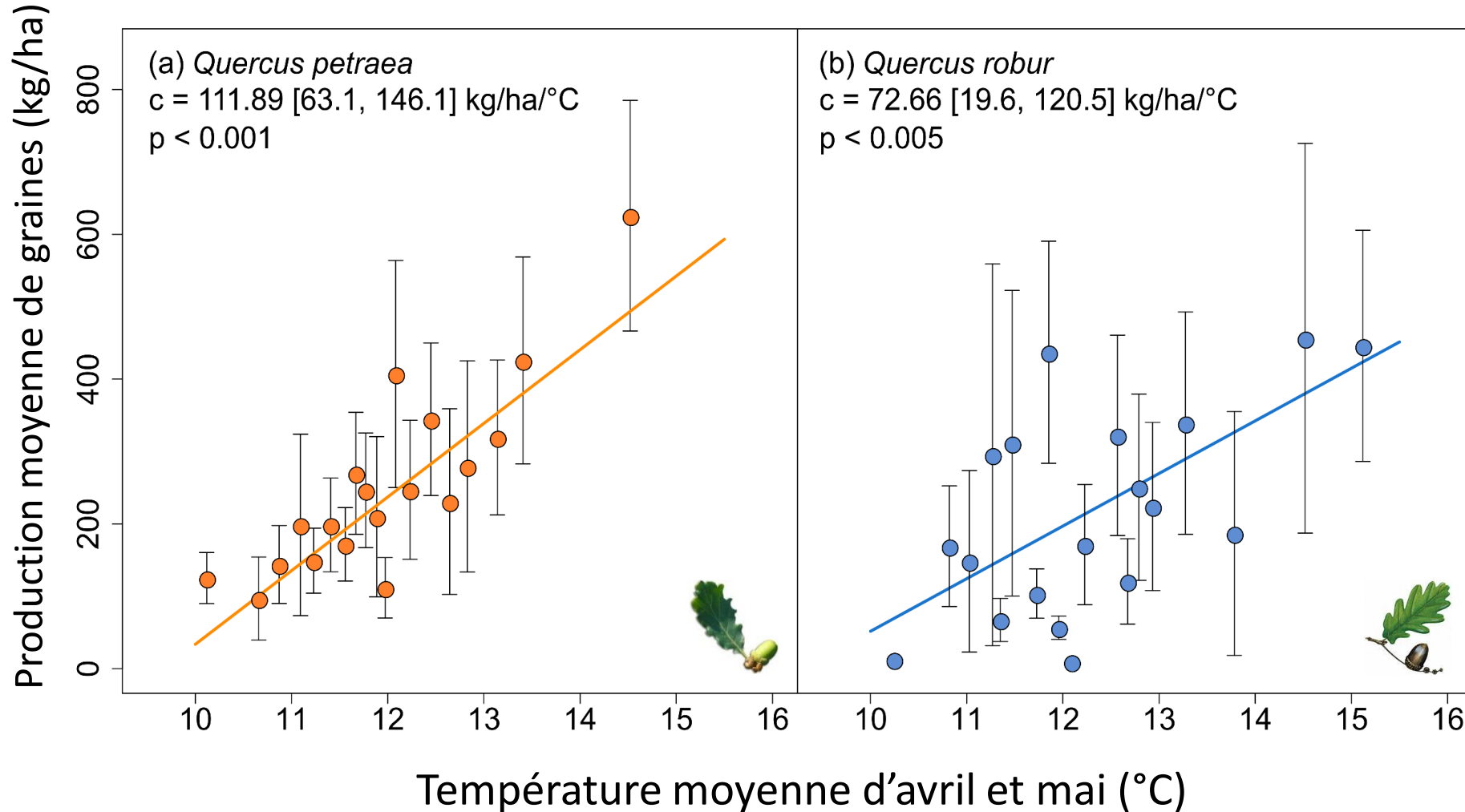
Changement climatique ?

Consommateurs – chaîne trophique
Régénération
Dynamique des communautés forestières

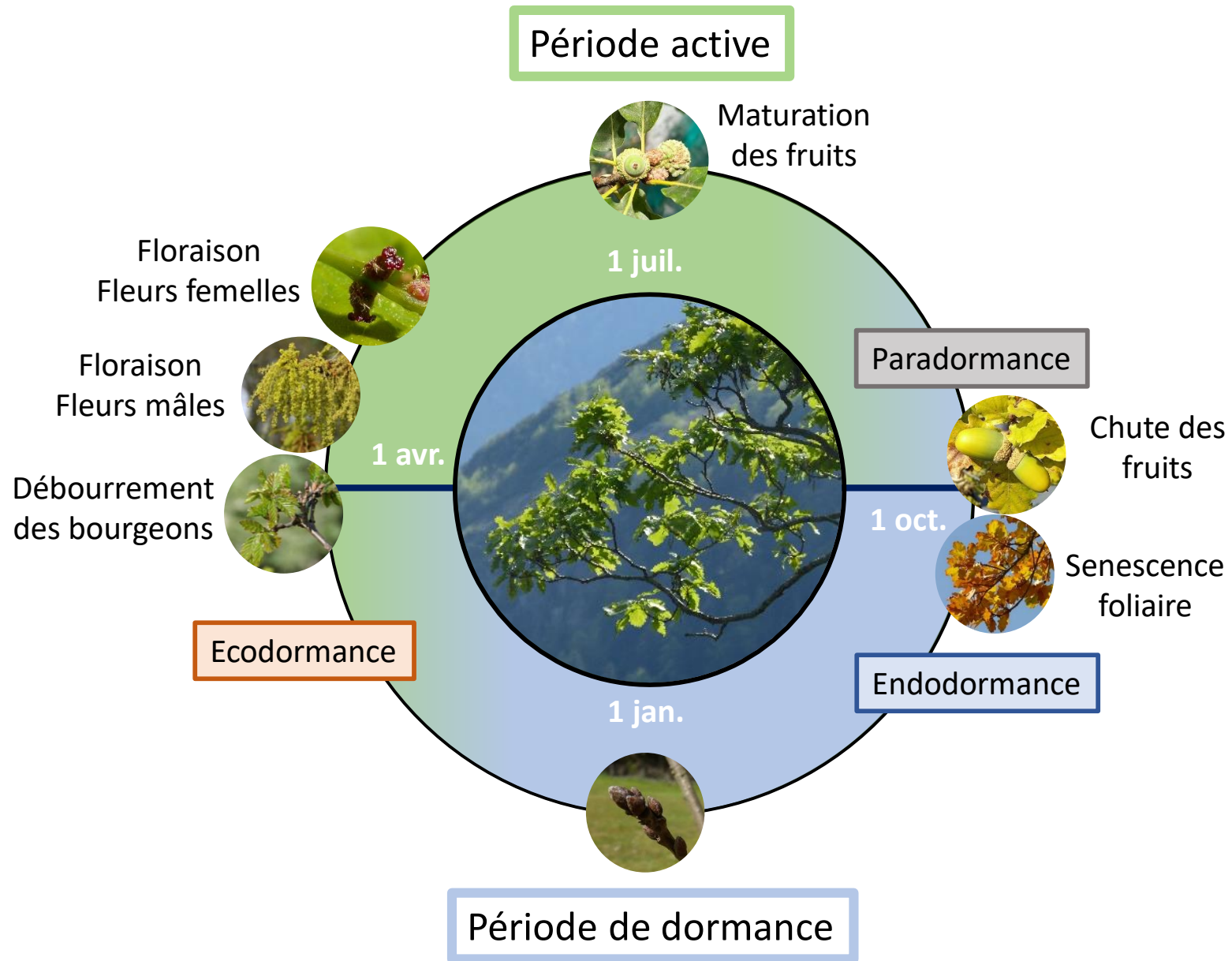
La reproduction sensible au climat: exemple du chêne



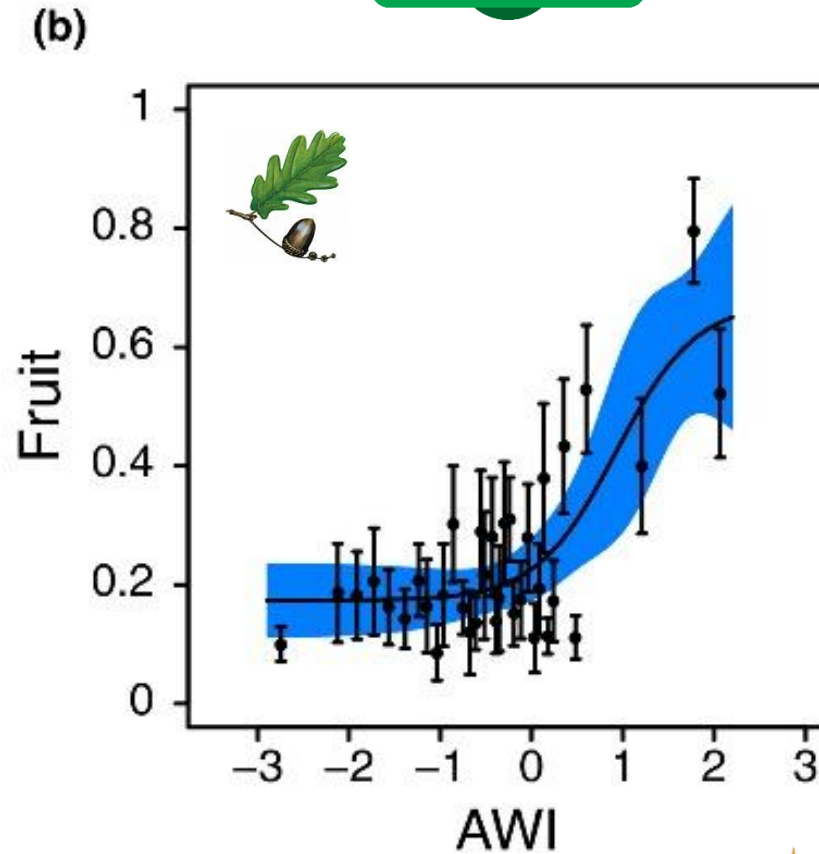
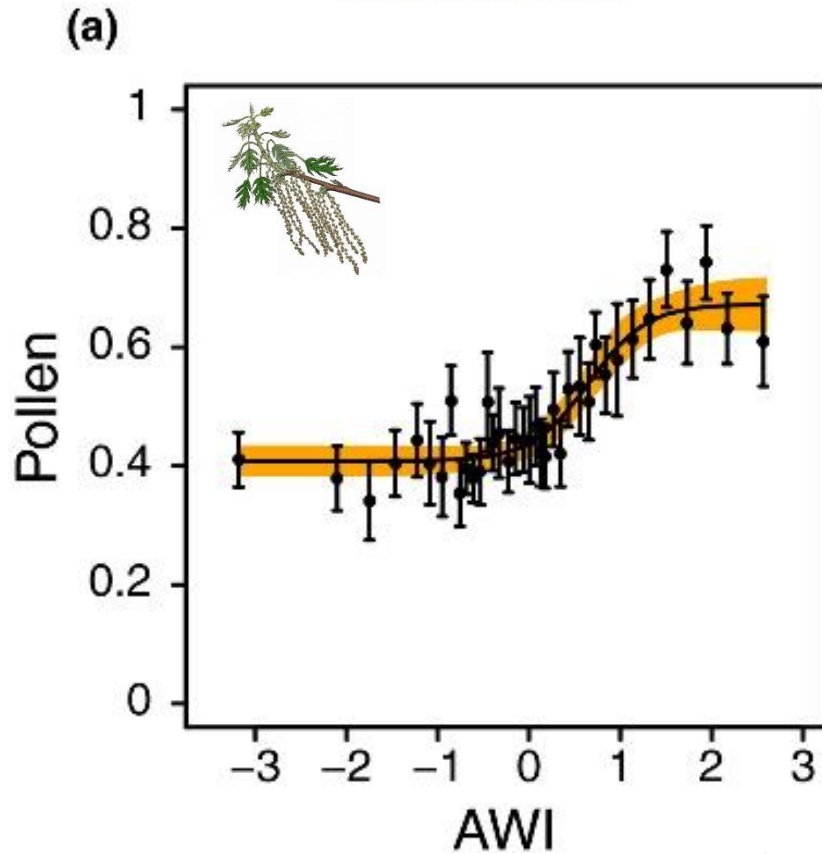
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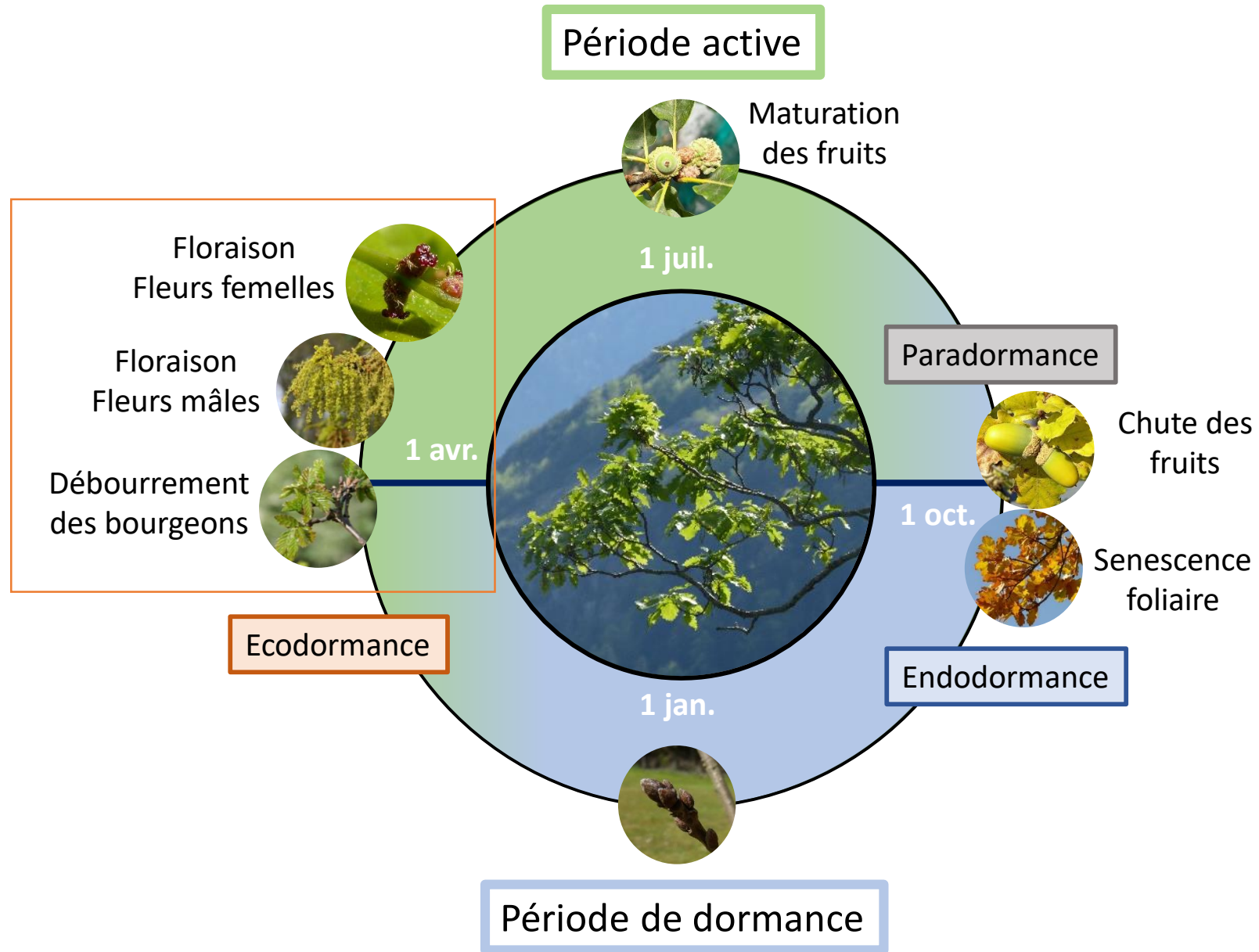
La reproduction sensible au climat: exemple du chêne



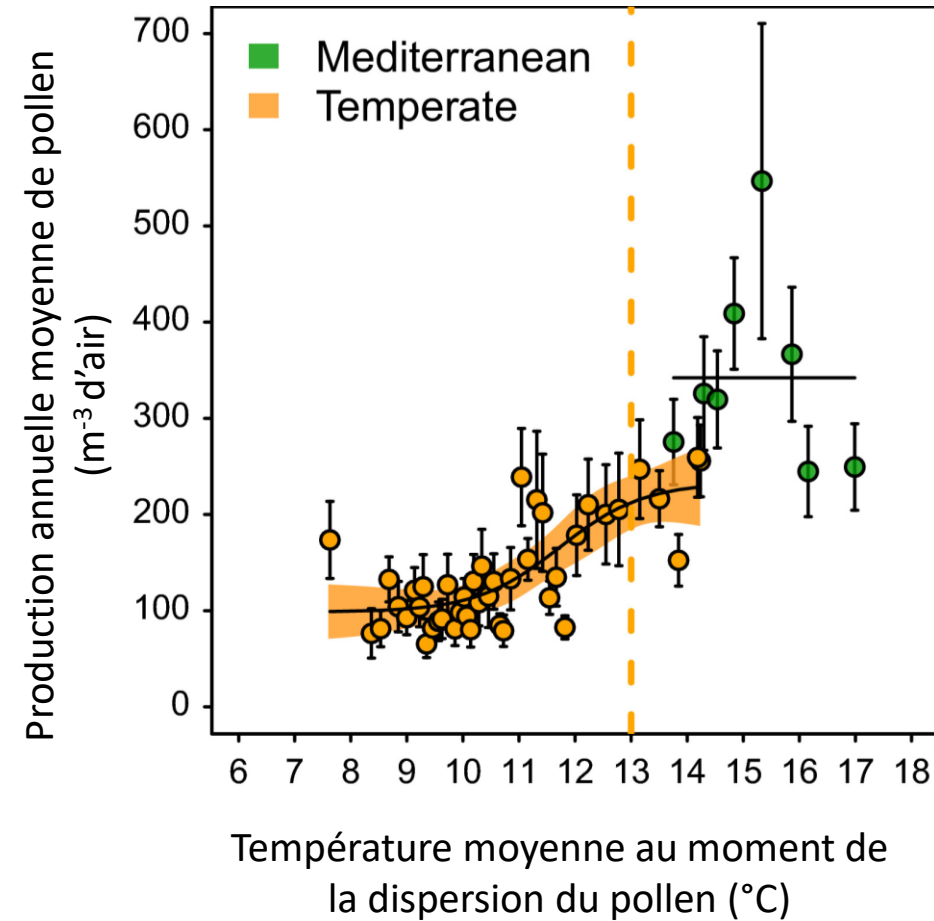
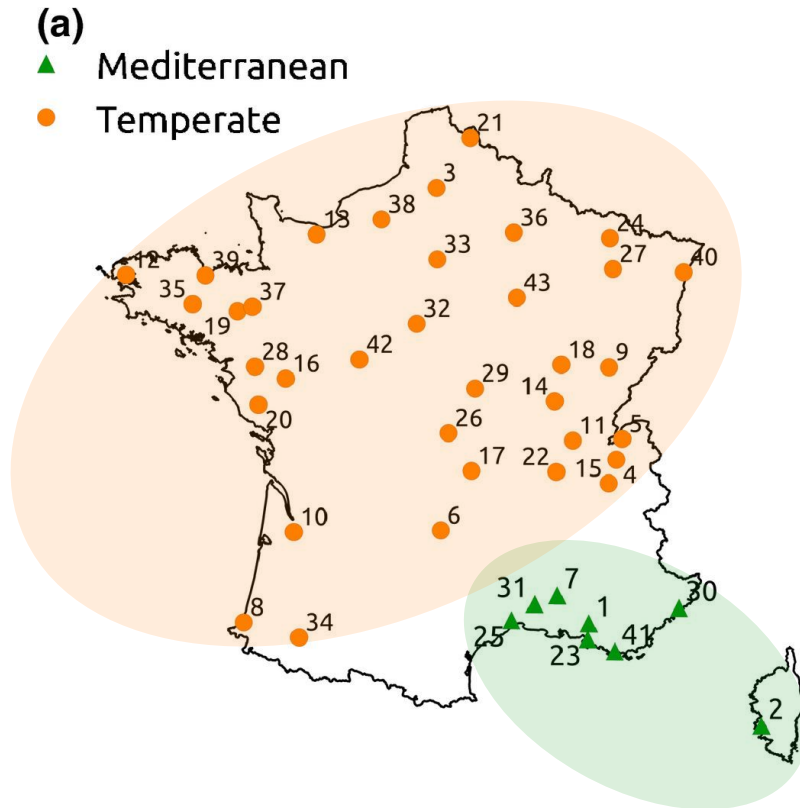
La reproduction sensible au climat: exemple du chêne



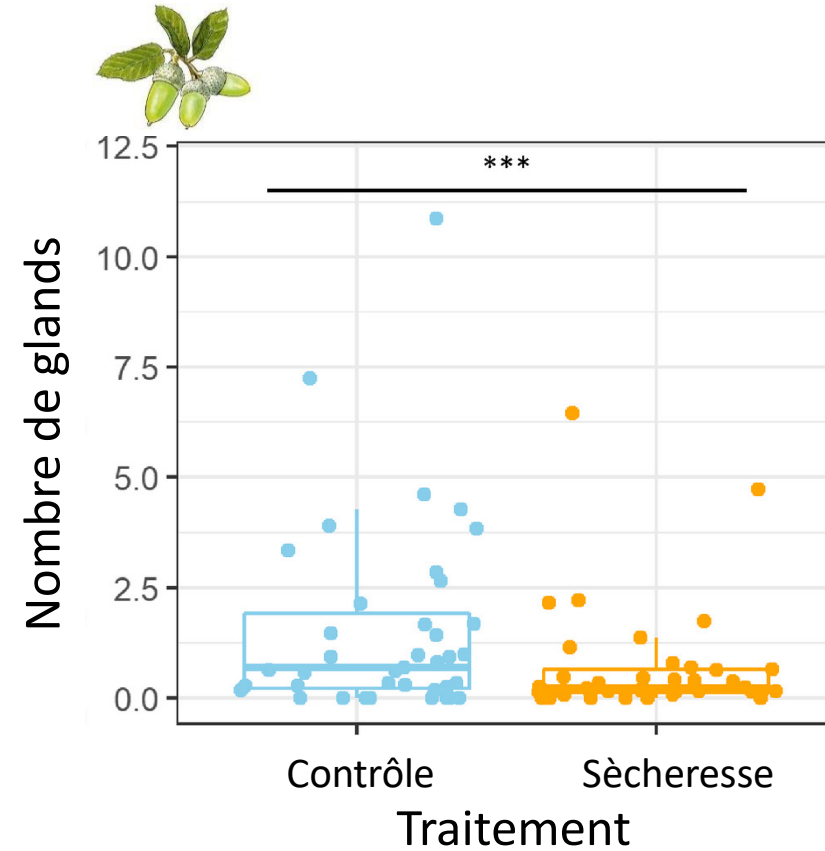
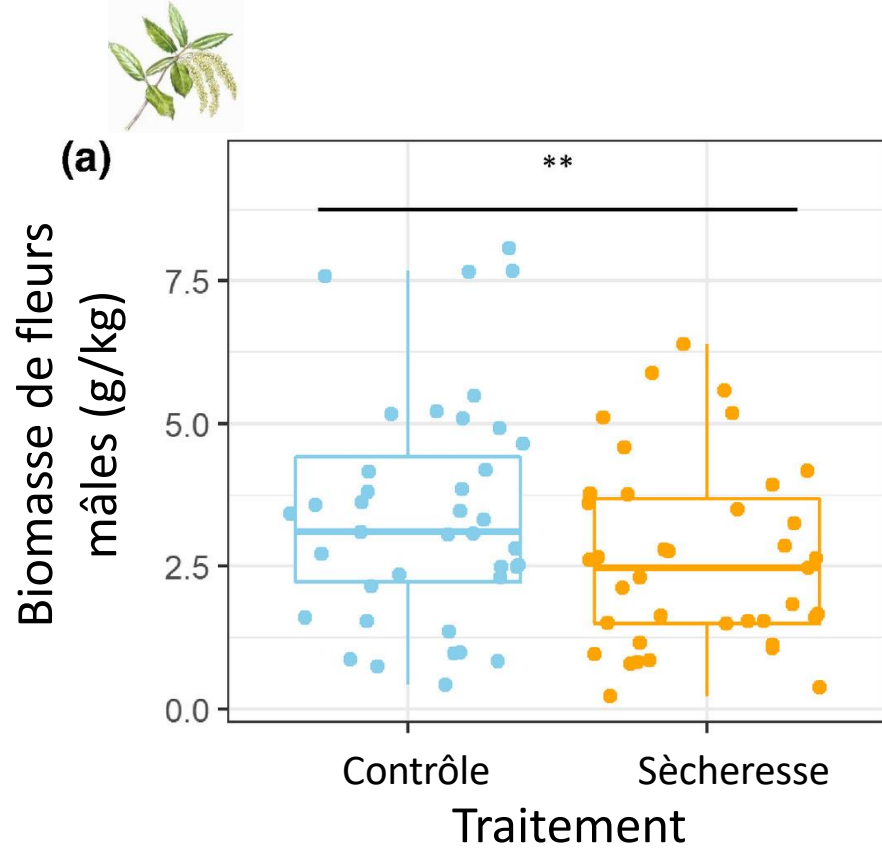
La reproduction sensible au climat: exemple du chêne



La reproduction sensible a climat: exemple du chêne

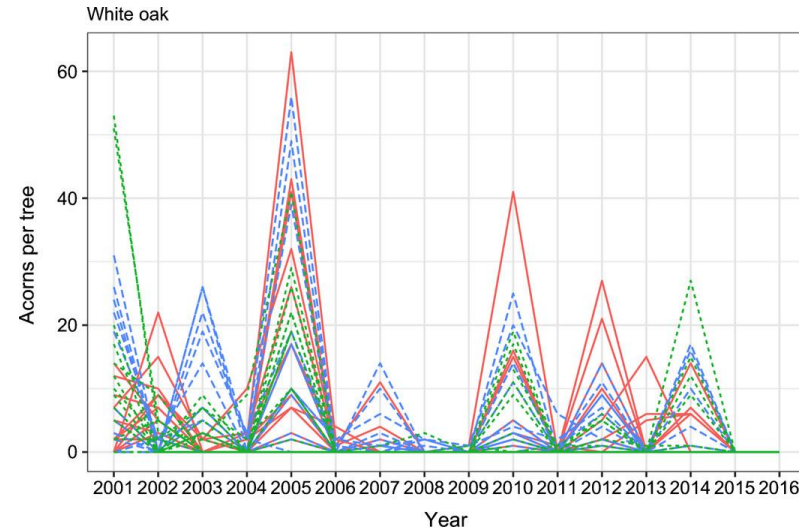


La reproduction sensible au climat: exemple du chêne



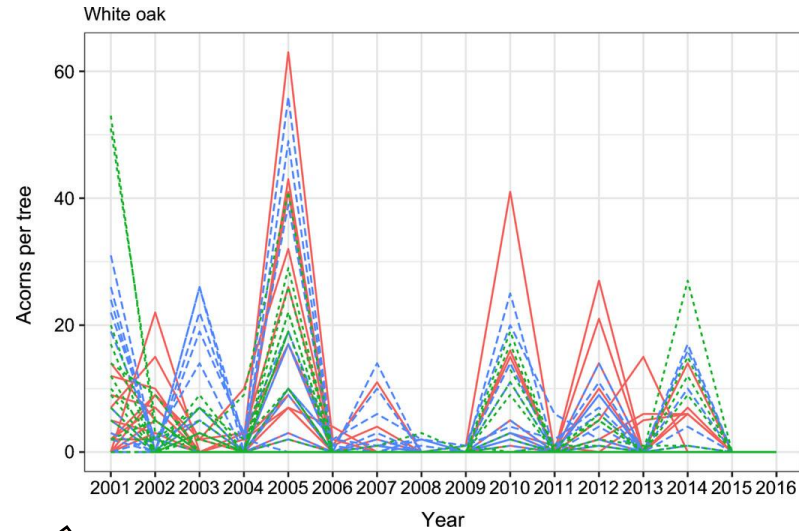
Site de Puéchabon
(CNRS)

La reproduction sensible au climat: exemple du chêne

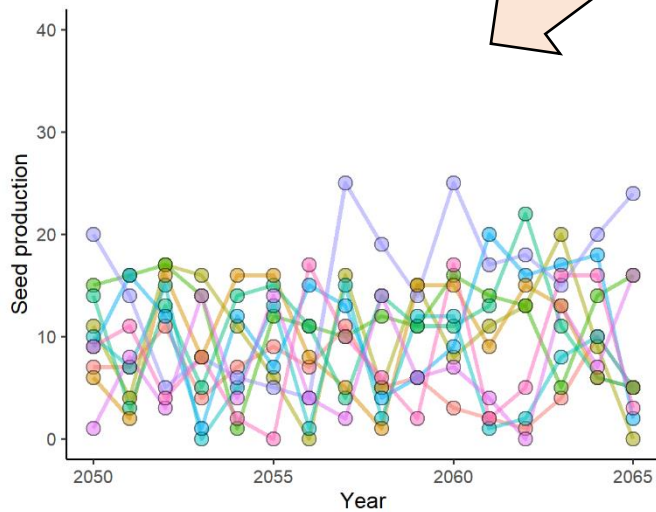


- ➔ Effet positif des températures sur la fructification et la floraison des chênes de milieux tempérés.
- ➔ Rôle important de la phénologie foliaire et florale.
- ➔ Effet négatif de la sécheresse sur la fructification en milieux méditerranéens.

Effet du changement climatique sur le masting

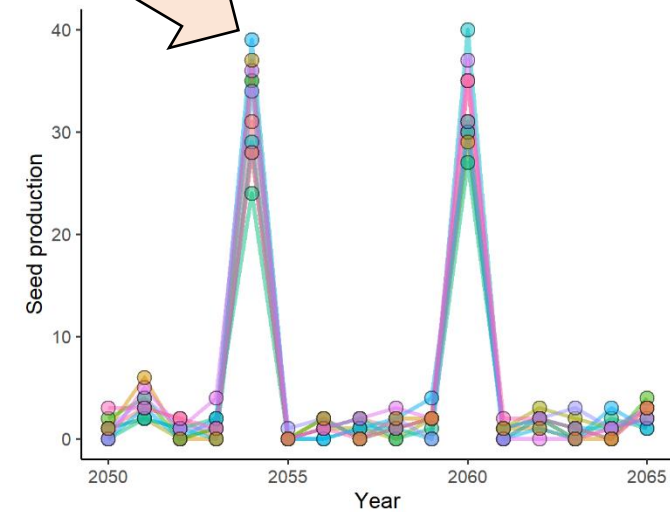


Bogdziewicz
et al. 2018



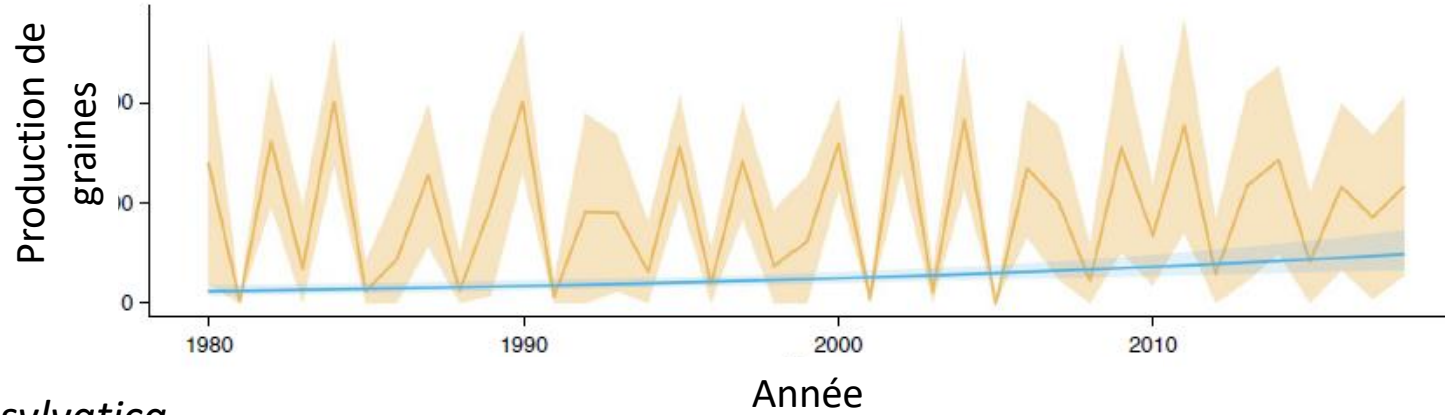
Vers des fructifications régulières ?

Changement climatique ?

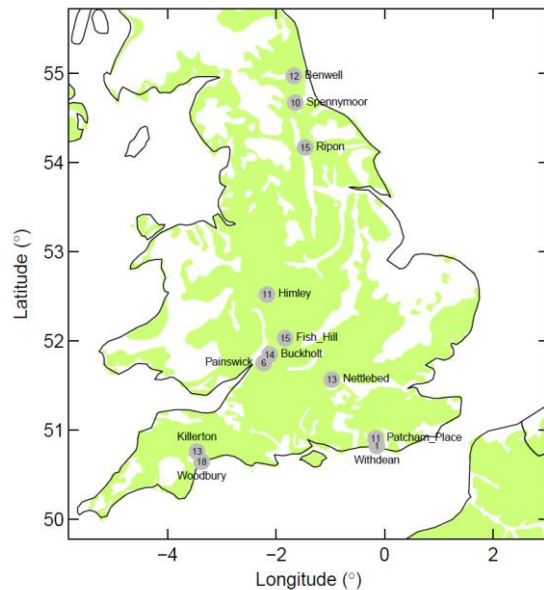


Vers des fructifications massives et plus rares ?

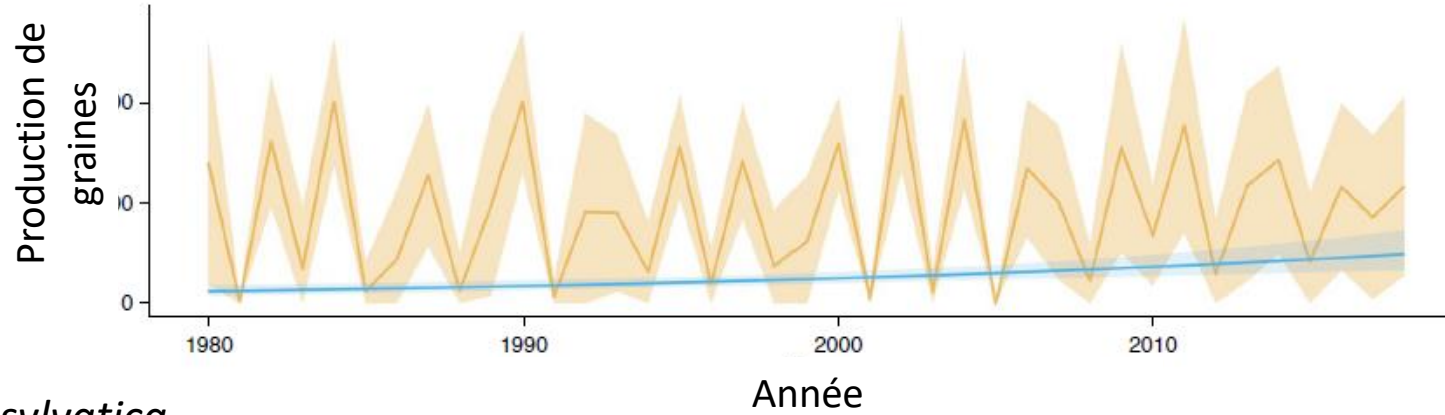
Effet du changement climatique sur le masting



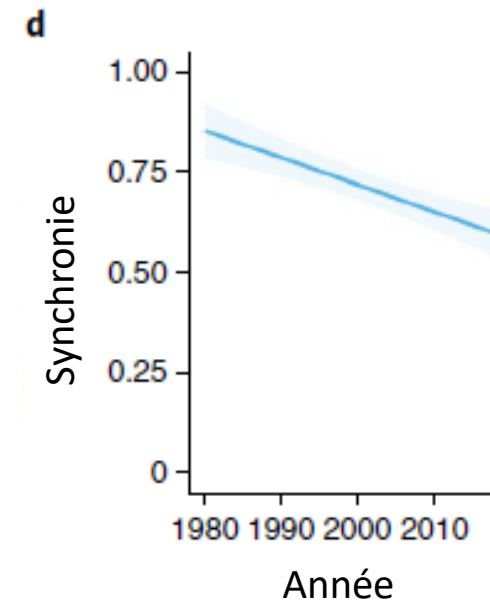
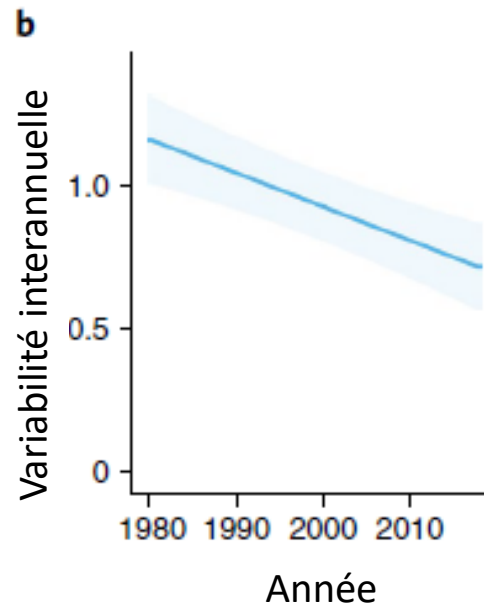
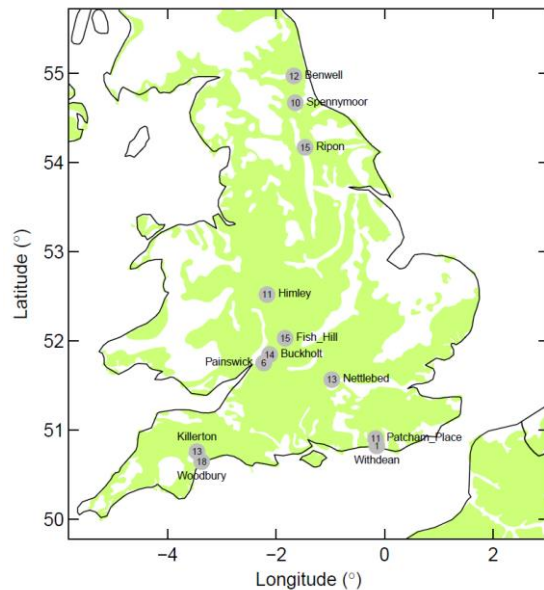
Fagus sylvatica
39 années de suivi



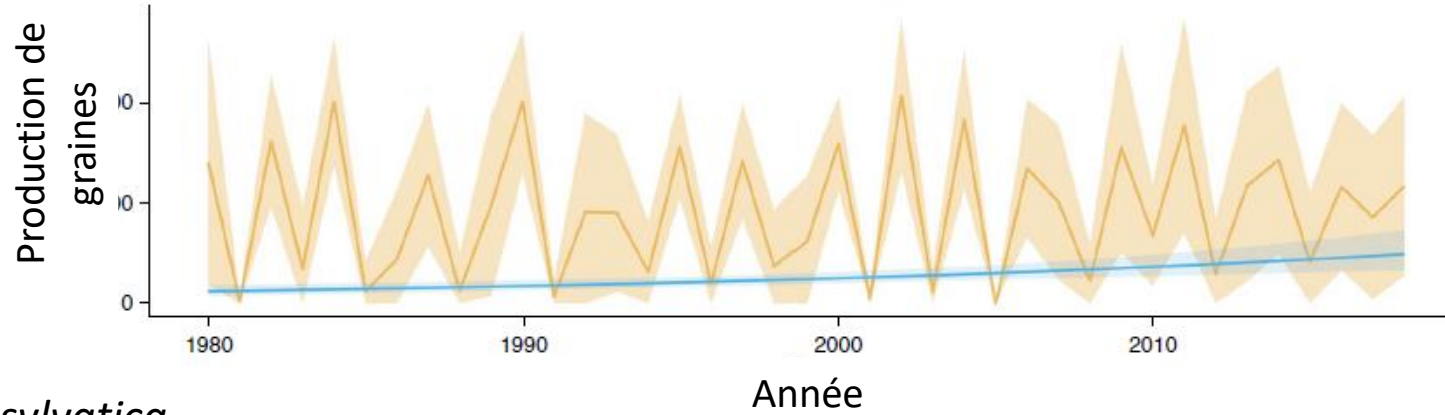
Effet du changement climatique sur le masting



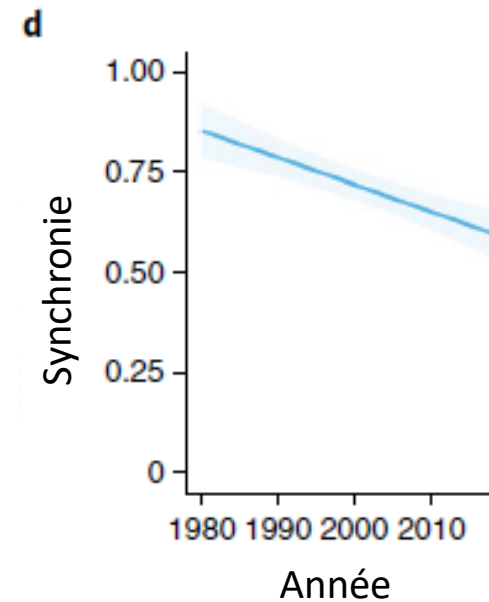
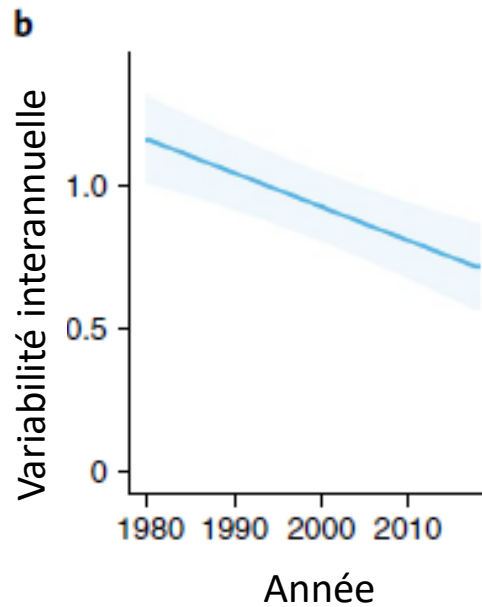
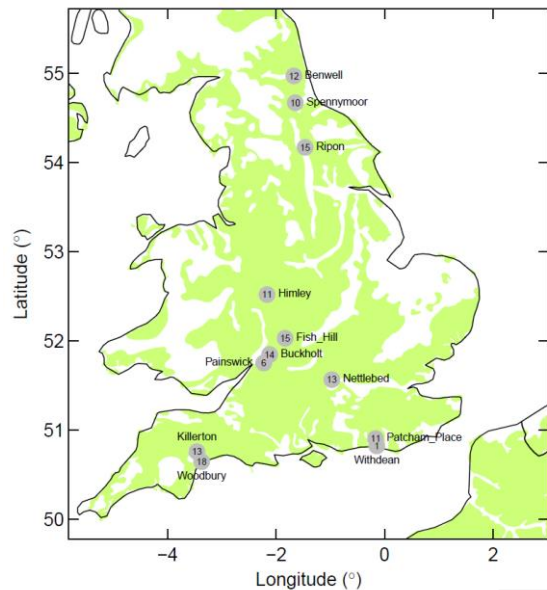
Fagus sylvatica
39 années de suivi



Effet du changement climatique sur le masting

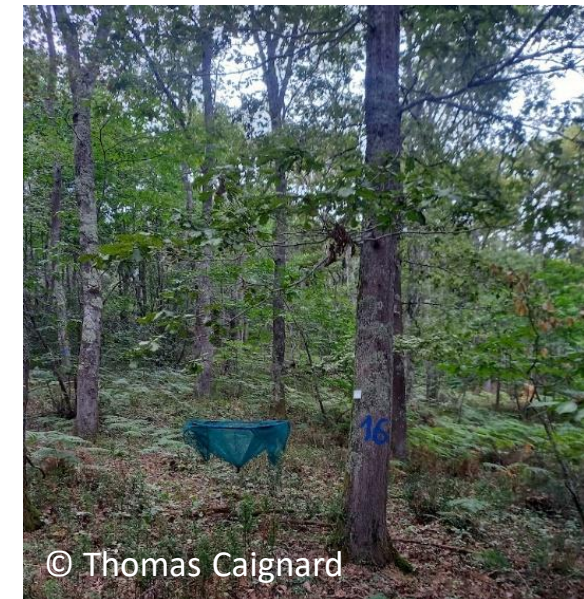
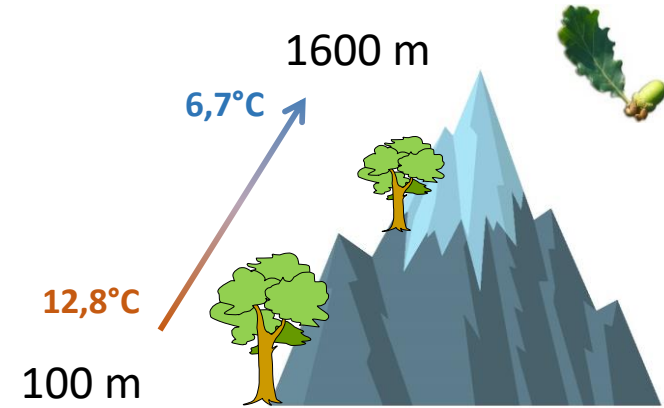
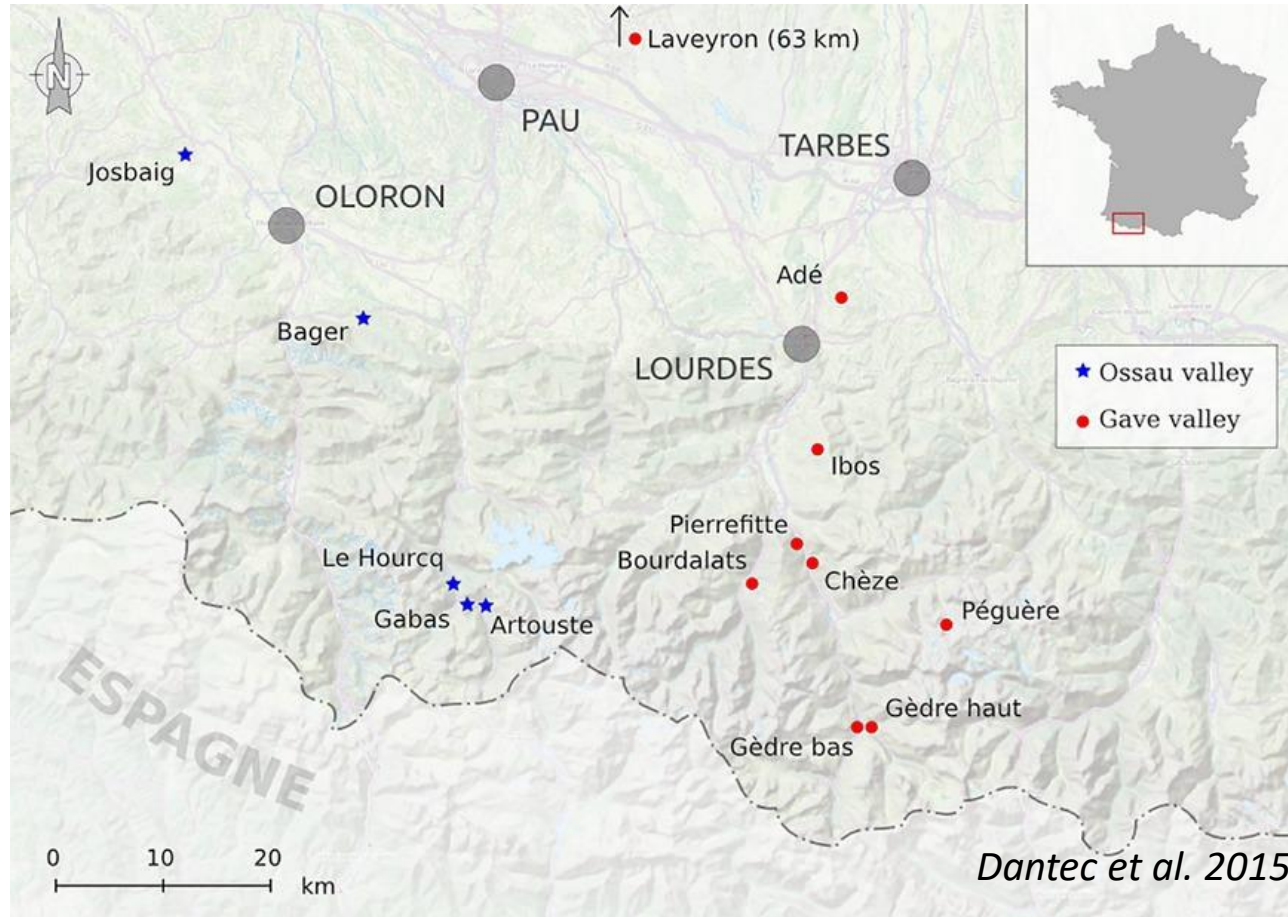


Fagus sylvatica
39 années de suivi



Diminution de l'intensité du masting au cours du temps

Impact du masting sur les écosystèmes

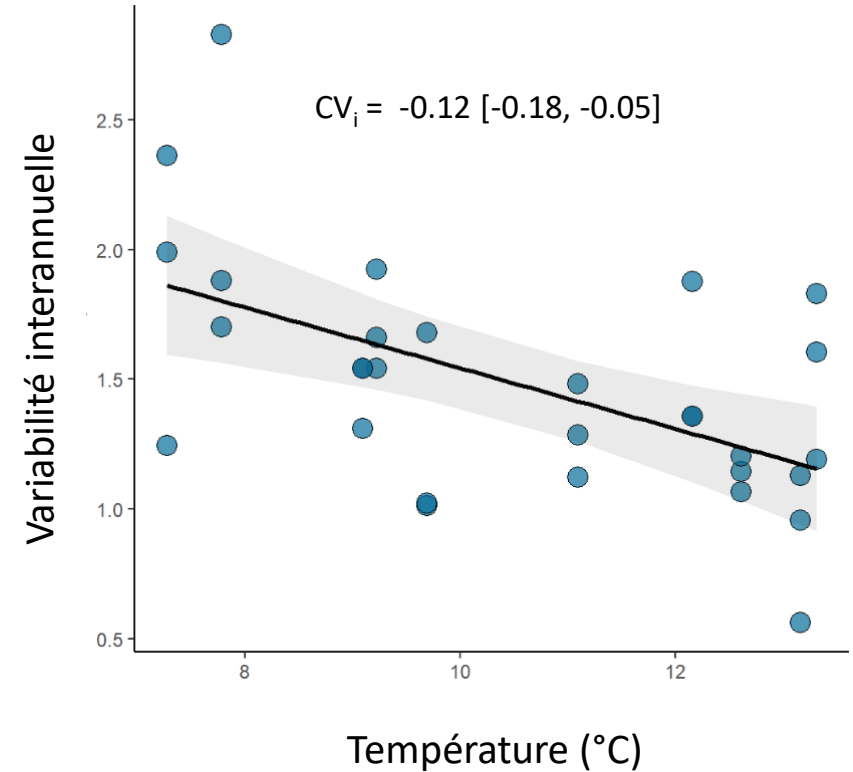
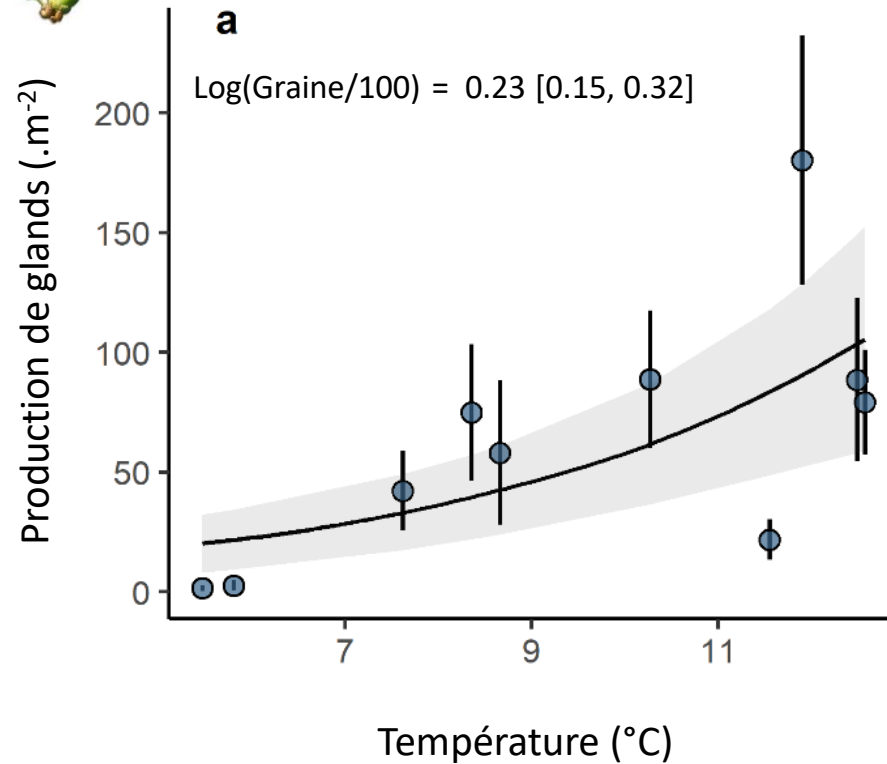
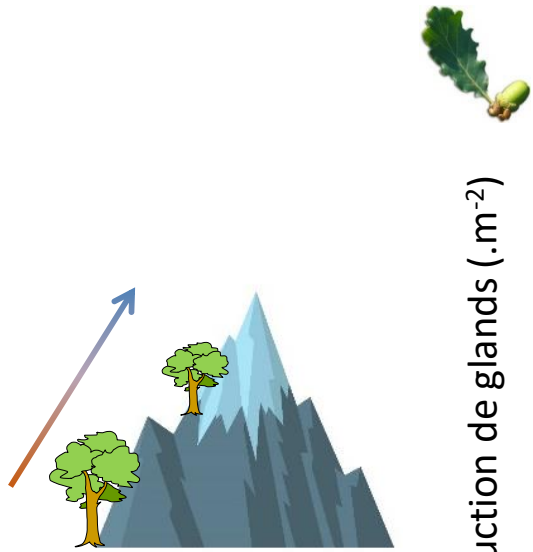


© Thomas Caignard

Ibos – 387m d'altitude

- ➔ 10 populations de chênes sessiles
- ➔ 5 altitudes de 100 à 1600m d'altitude

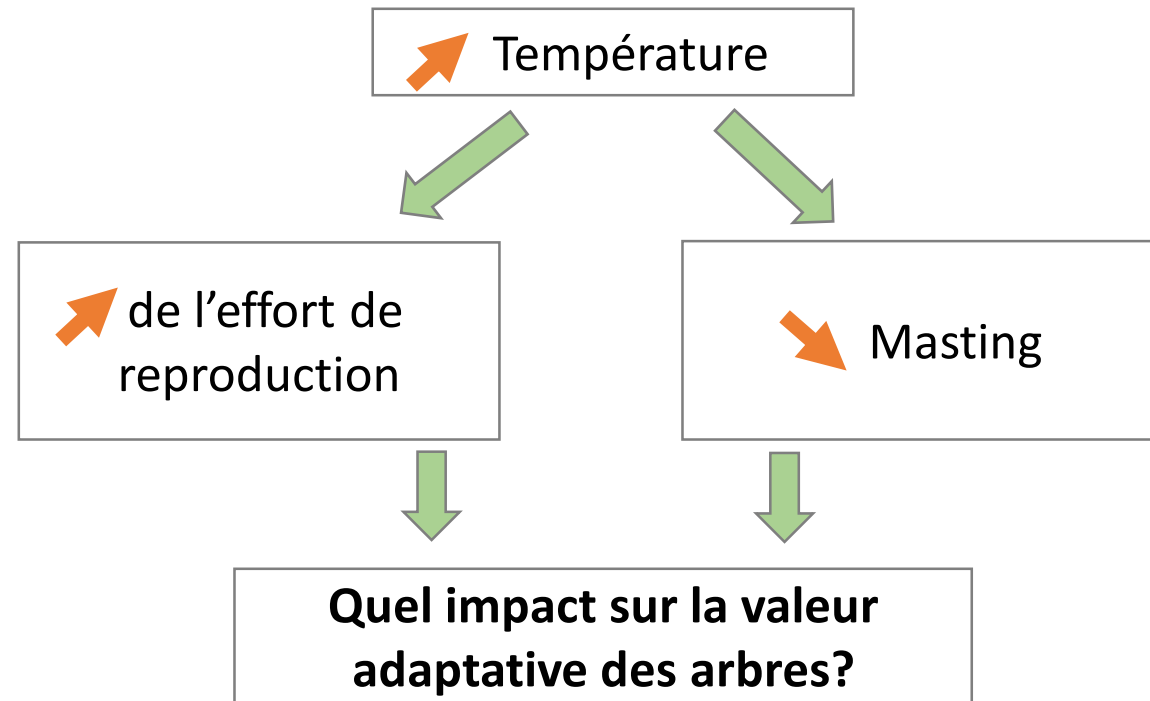
Effet du changement climatique sur le masting



➔ Augmentation de la production de glands avec la température

➔ Diminution de l'intensité du masting

Effet du changement climatique sur le masting



- ➔ Comprendre les mécanismes physiologiques associés au masting (Allocation des ressources, signaux hormonaux)
- ➔ Etudier les déterminismes génétiques de ce phénomène.

Etude des causes proximales

Causes proximales

1. Le rôle des ressources de l'arbre sur le masting

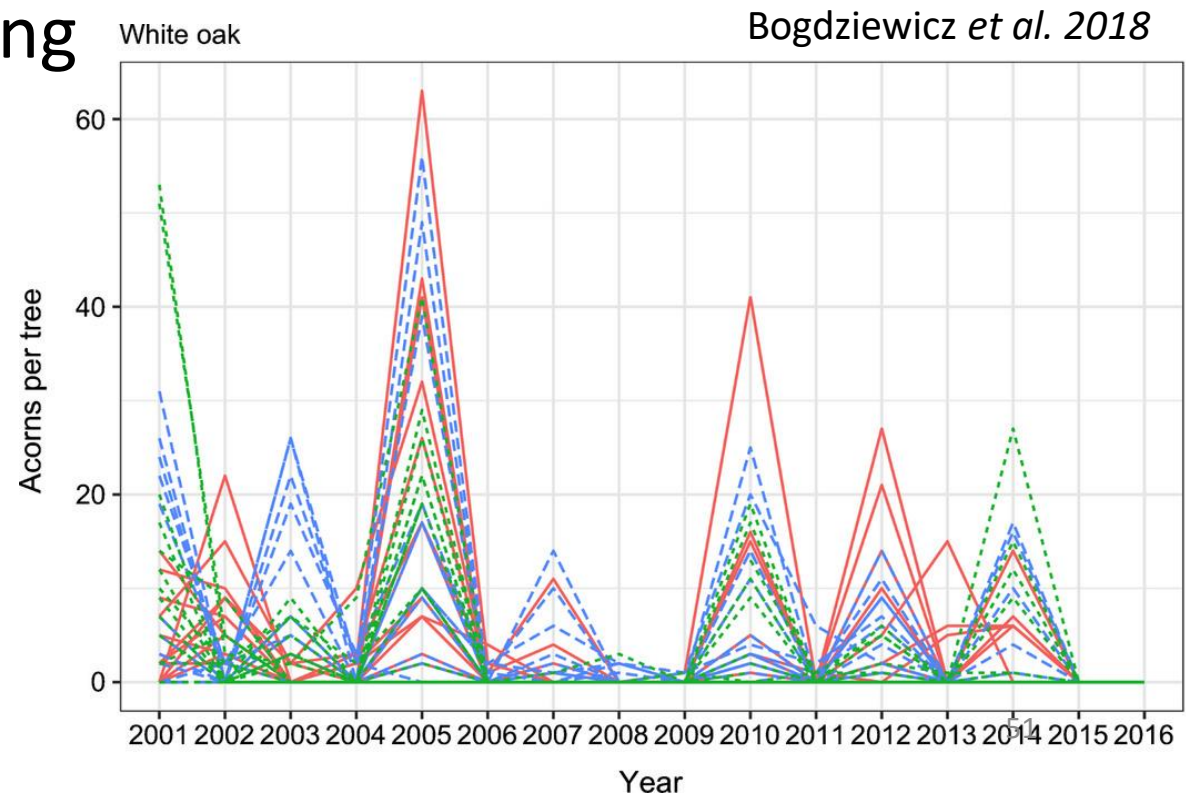
1. « Resource matching »
2. « Resource Budget Model »

2. Signaux exo et endogène au masting

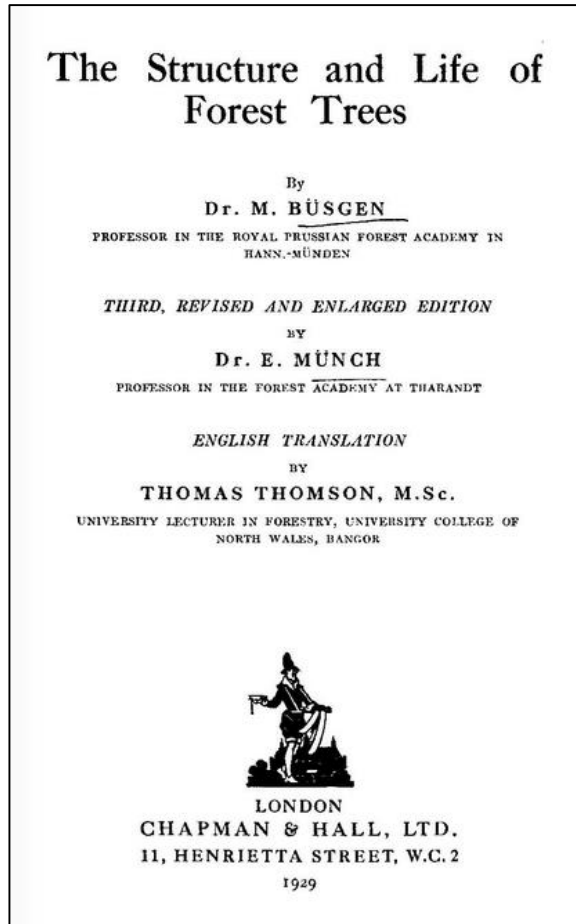
1. Signal climatique
2. Signal pollinique
3. Réunification des théories

3. Nouvelles perspectives

1. Signal hormonal
2. Déterminisme génétique

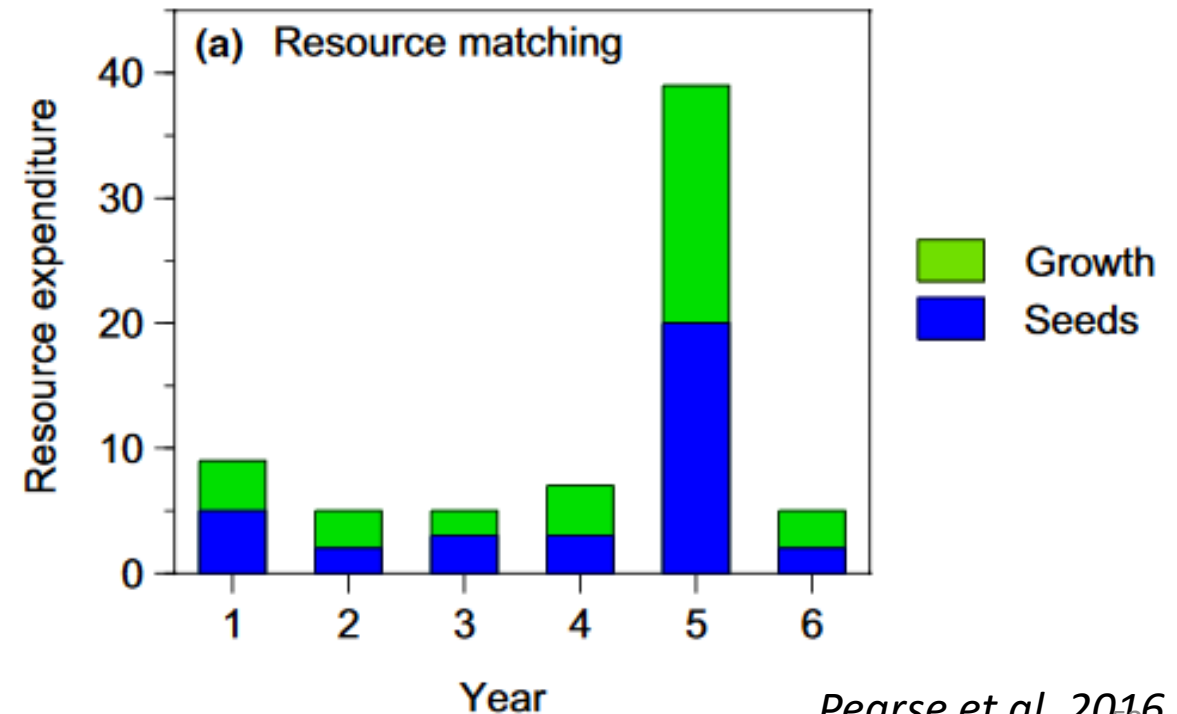


1.1. Causes proximales: Ressource matching

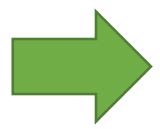


Büsgen & Münch –
The structure and life of forest trees (1929)

Nombre de fruits varie en fonction de la
disponibilité en ressource de l'année.
(Kelly 1994)

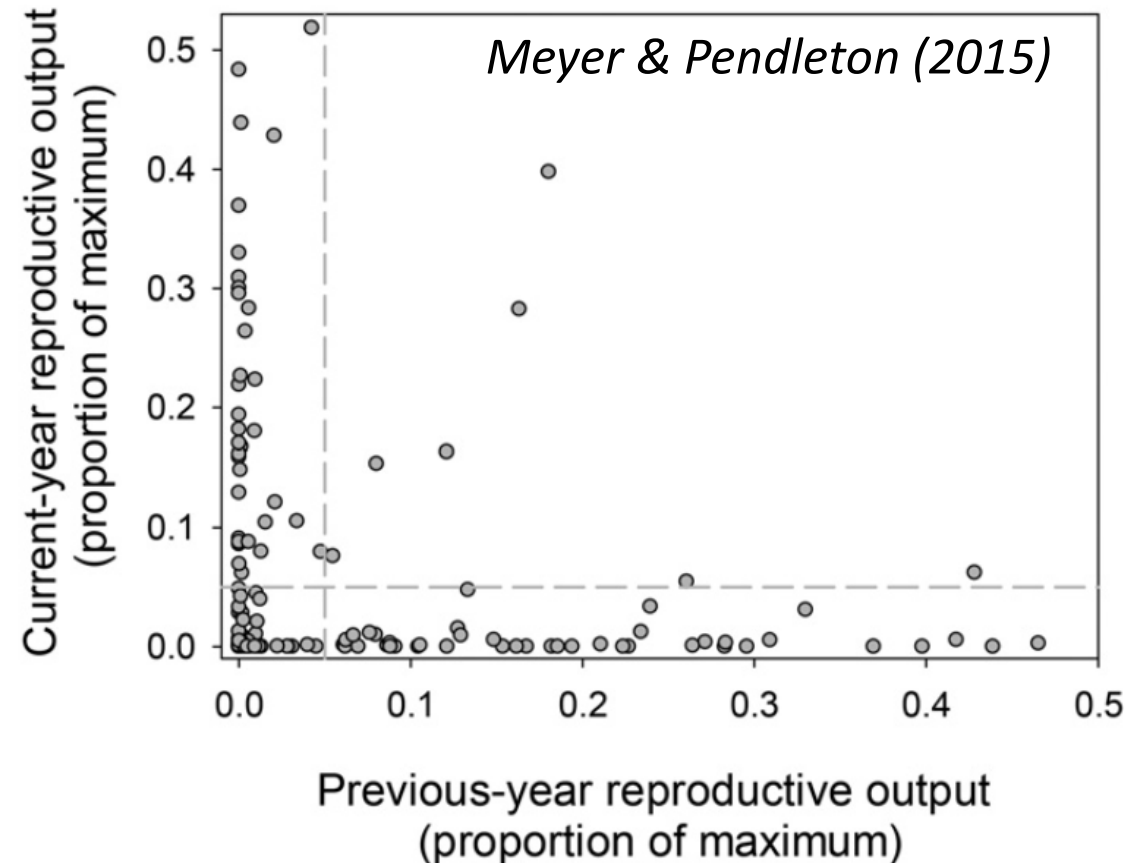


1.1. Causes proximales: Ressource matching

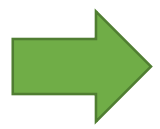


Nombre de fruits varie en fonction de la disponibilité en ressource de l'année. (*Kelly 1994*)

➤ Autocorrélation temporelle négative



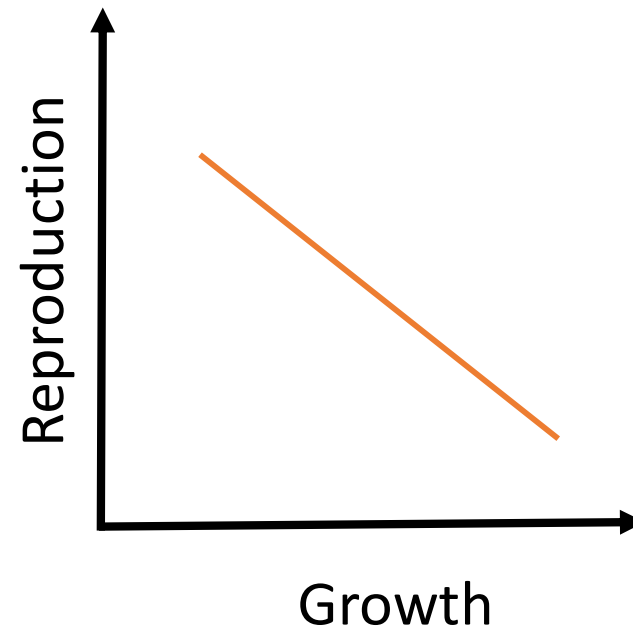
1.1. Causes proximales: Ressource matching



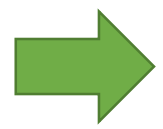
Nombre de fruits varie en fonction de la disponibilité en ressource de l'année. (*Kelly 1994*)

➤ Compromis Croissance/Reproduction est négatif pour la plupart des espèces de masting

- *Camarero et al. 2010*
- *Drobyshev et al. 2010*
- *Ishihara & Kikuzawa 2009*
- *Han et al. 2008*
- *Monks & Kelly 2006*
- *Silvertown & Dodd 1999*
- *Koenig & Knops 1998*

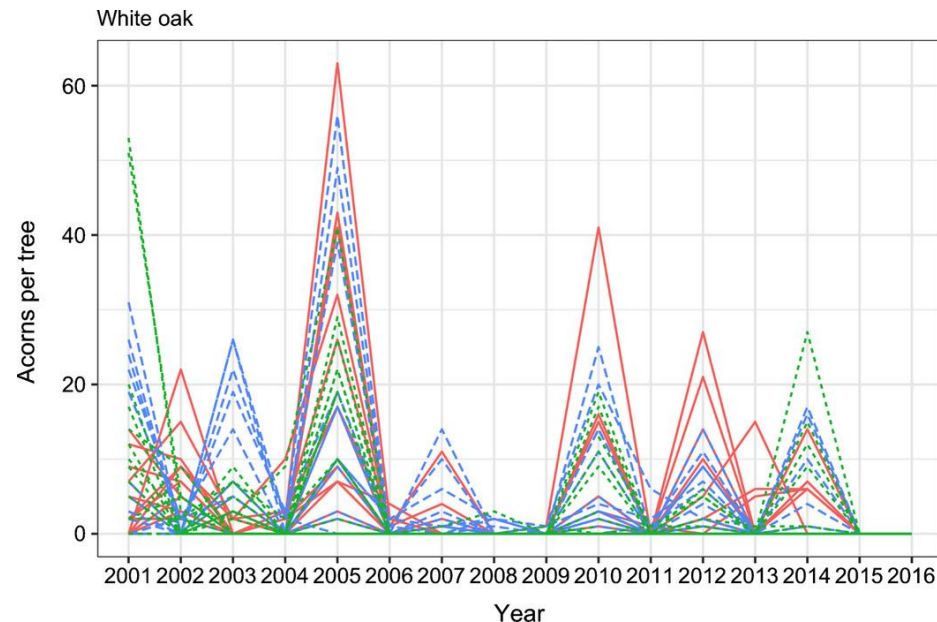


1.1.Causes proximales: Ressource matching

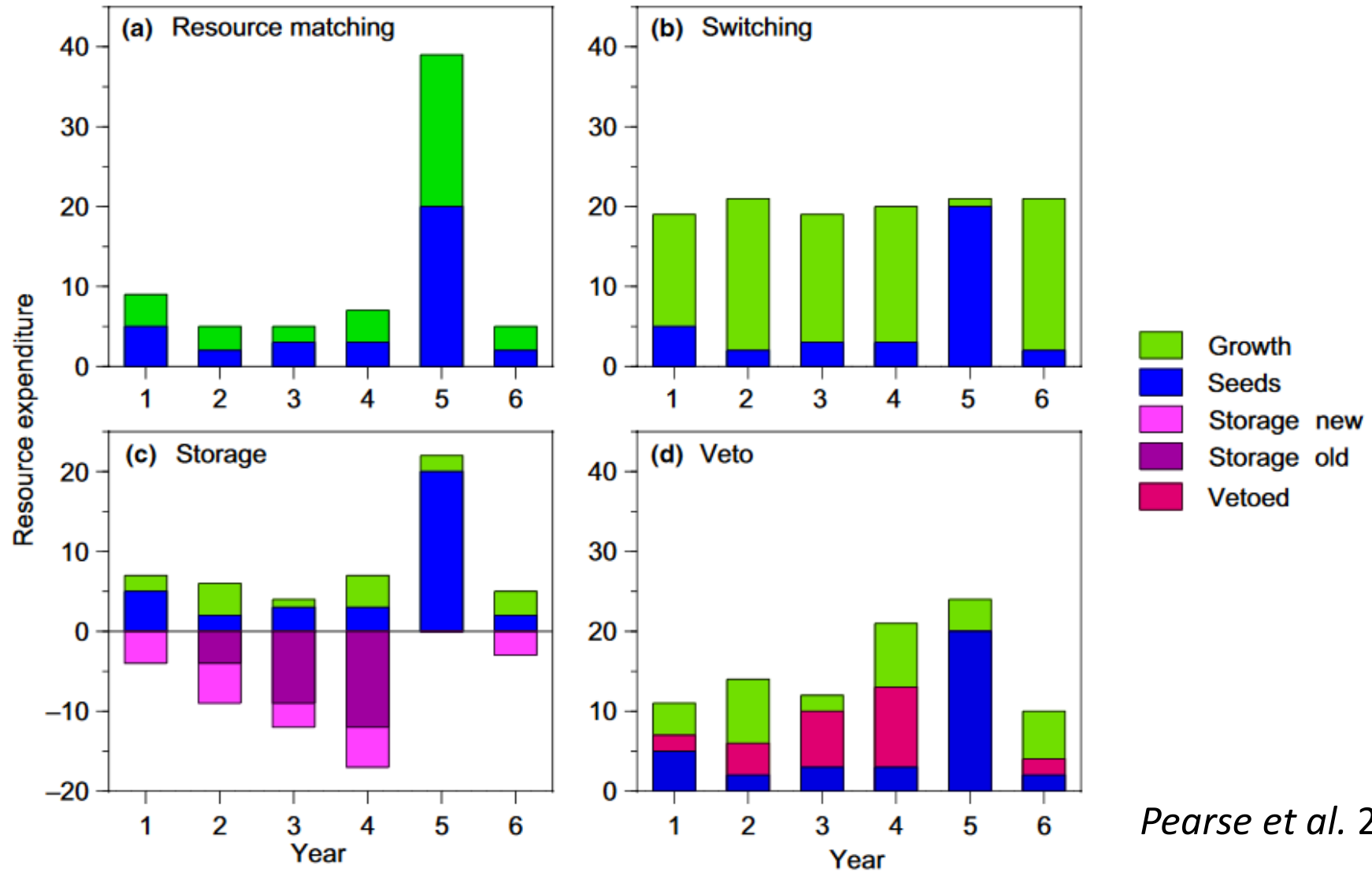


Nombre de fruits varie en fonction de la disponibilité en ressource de l'année. (*Kelly 1994*)

- L'hypothèse de « ressource matching » ne soutient pas le processus de masting en tant qu'avantage évolutif

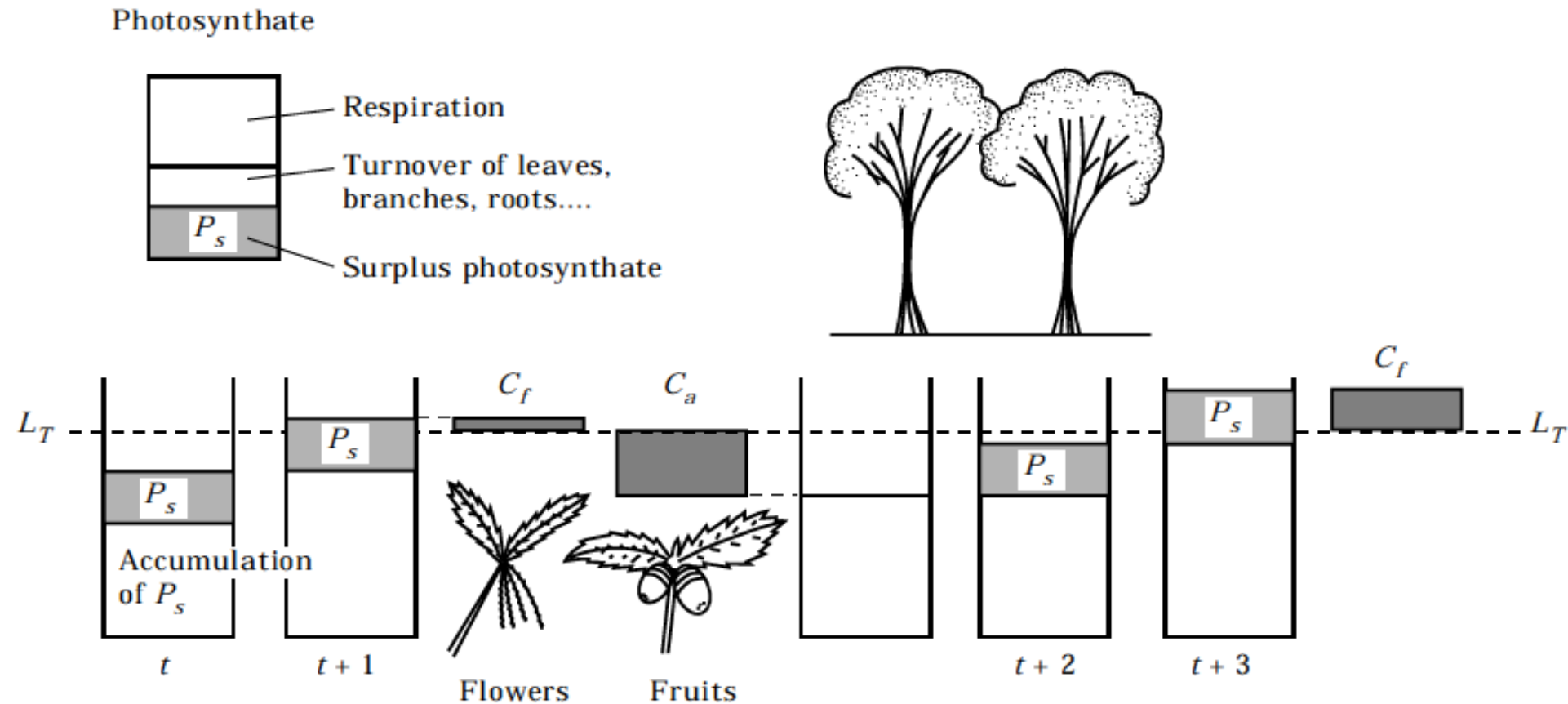


1. Causes proximales: 4 mécanismes



Pearse et al. 2016

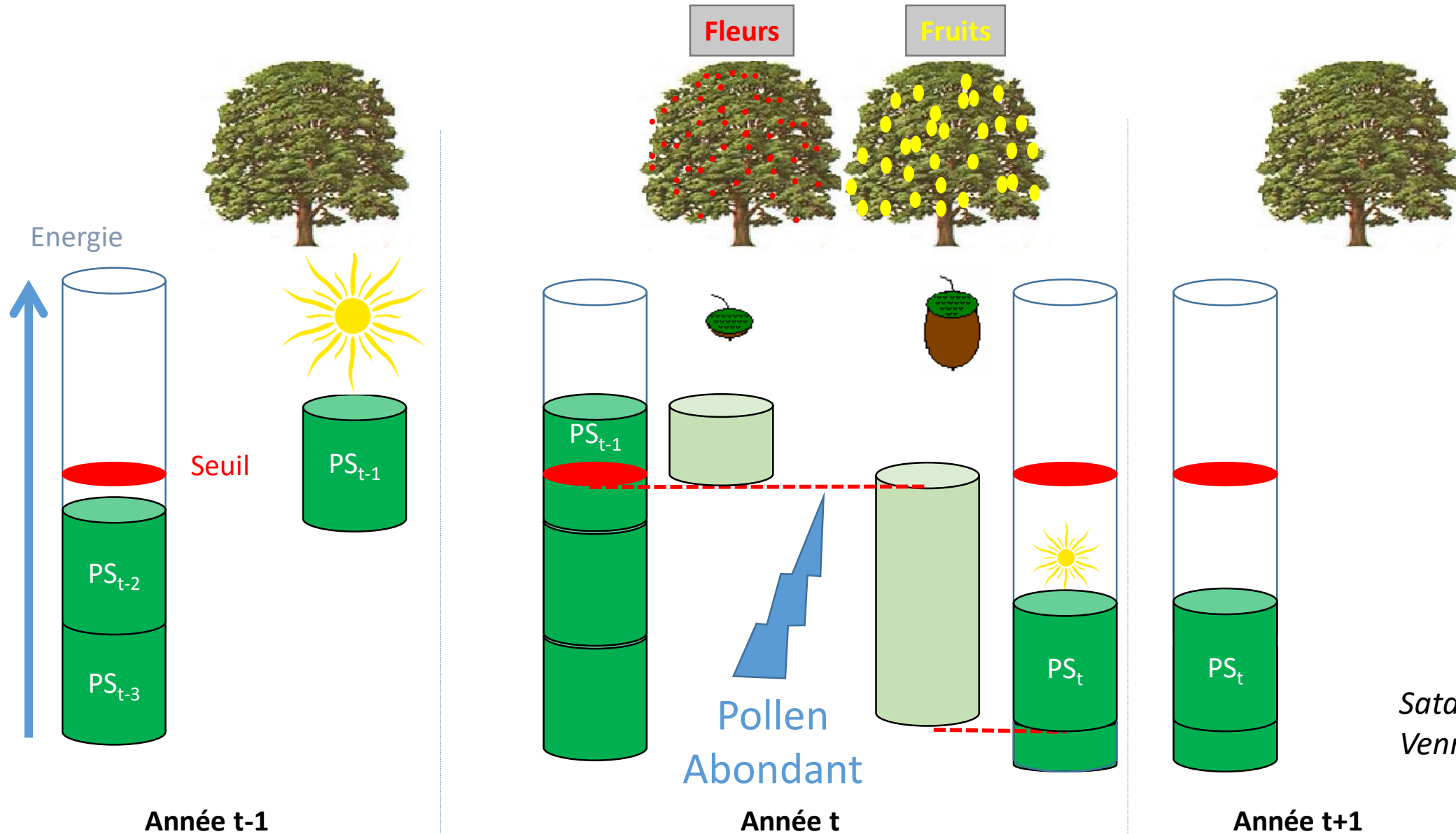
1.2. Causes proximales: Resource budget model



$$R_c = C_a / C_f$$

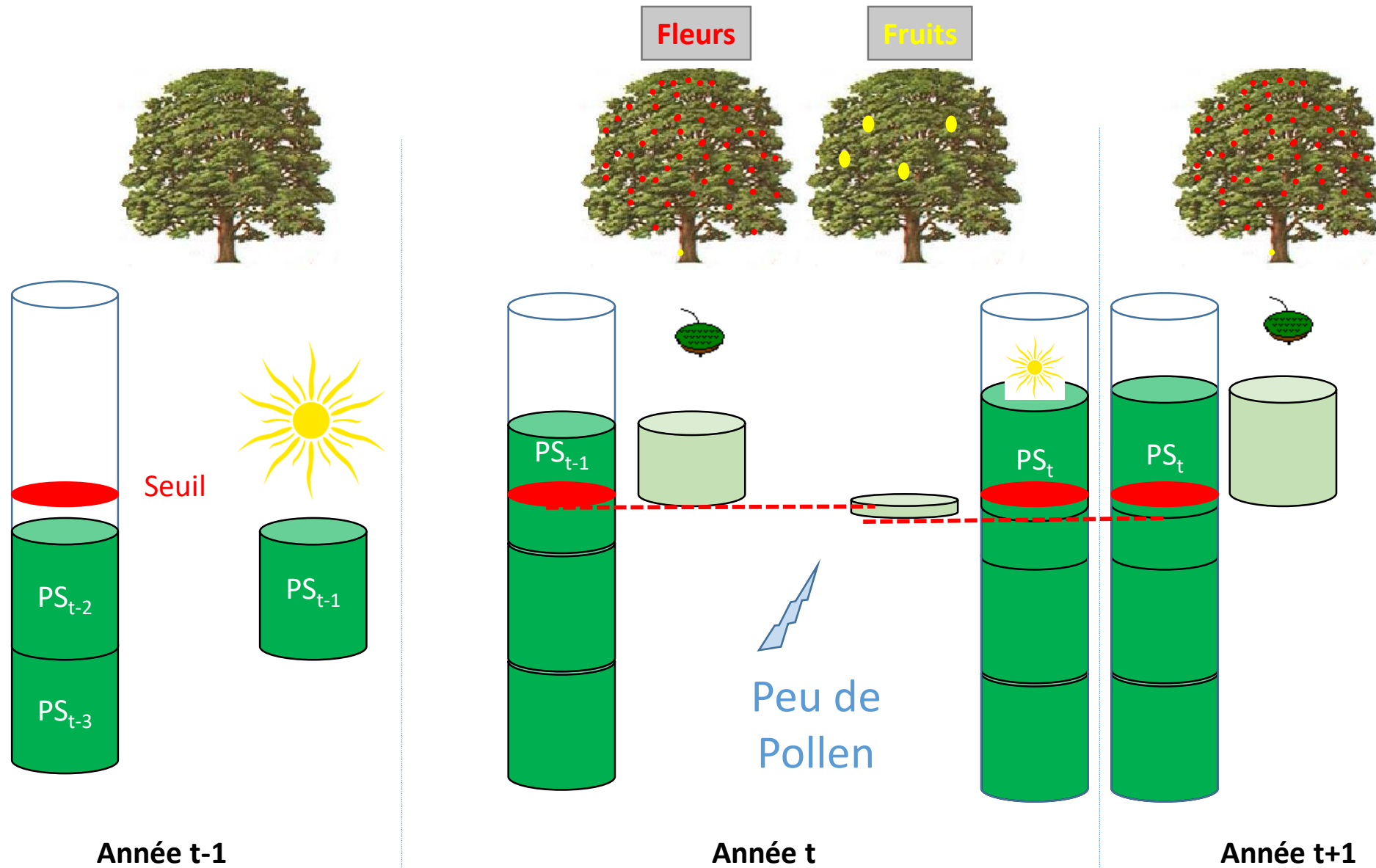
Isagi et al. 1997

1.2. Causes proximales: Resource budget model



Satake & Iwasa (2002)
Venner et al. (2016)

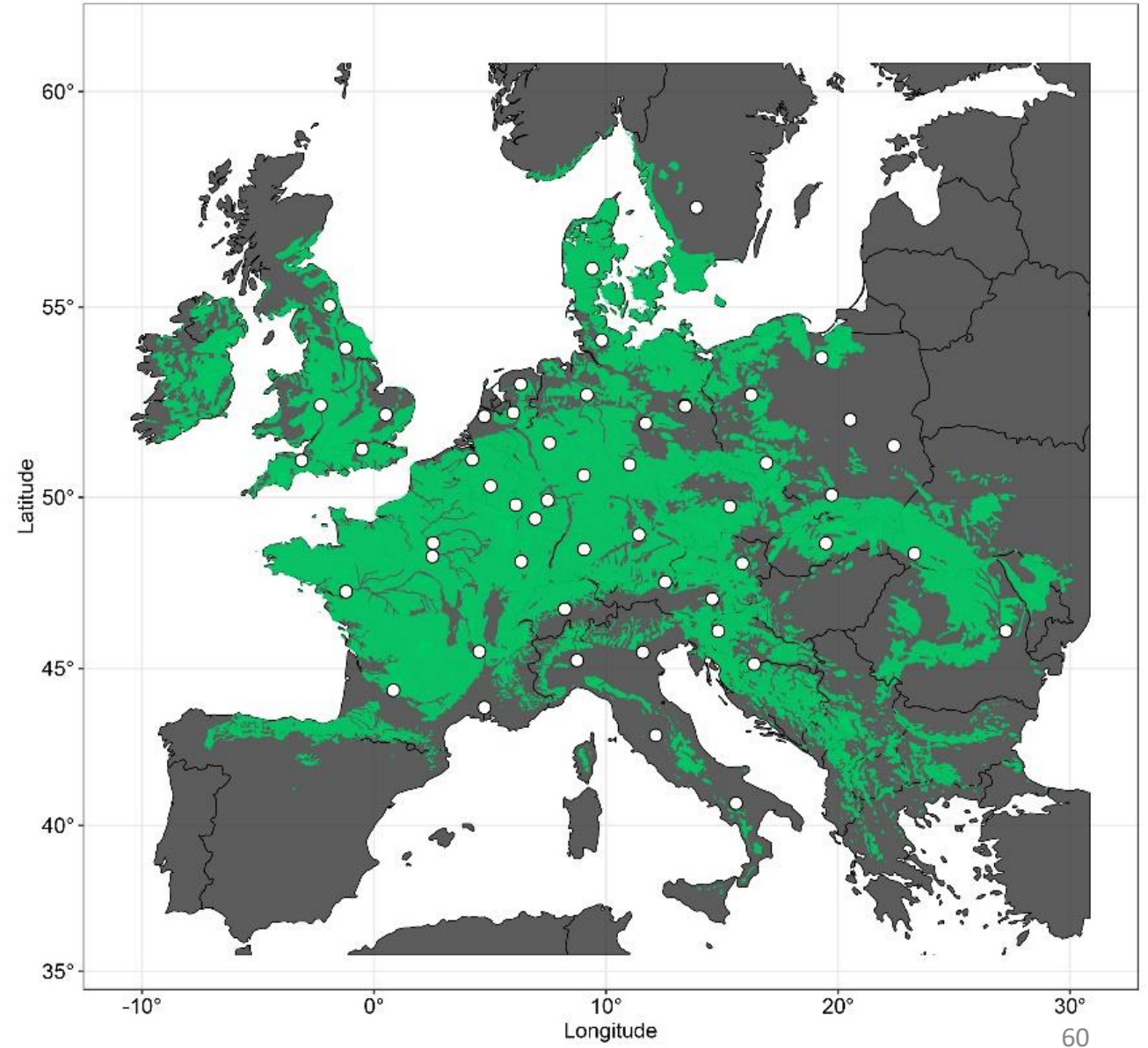
1.2. Causes proximales: Resource budget model



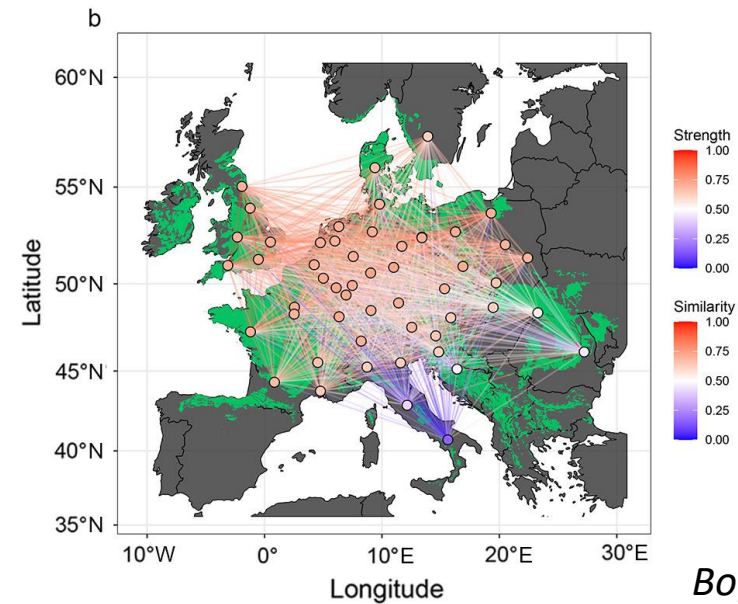
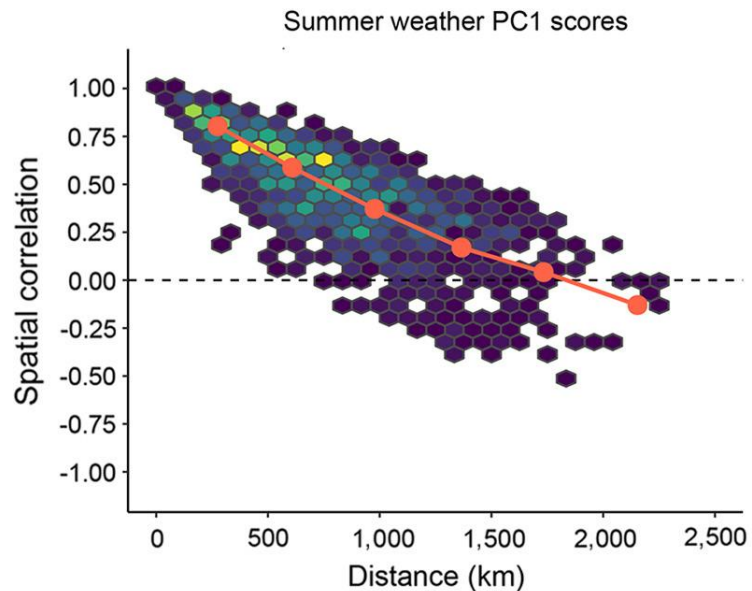
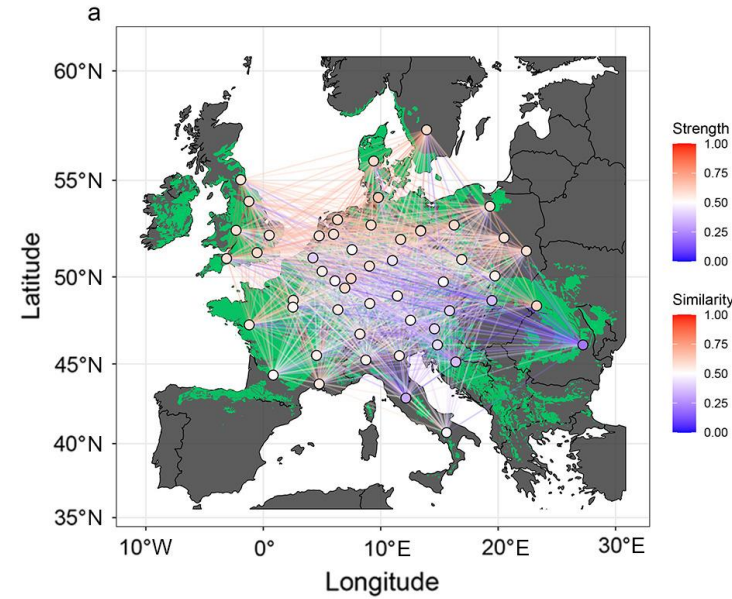
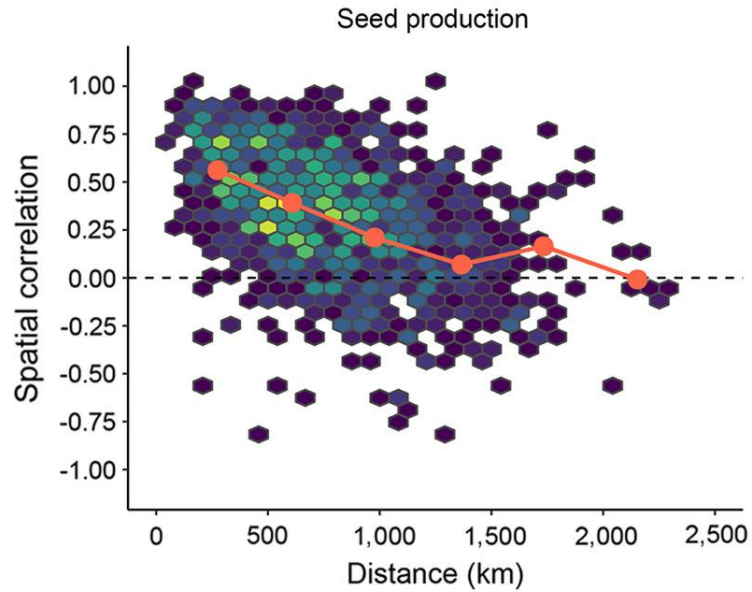
Satake & Iwasa (2002)
Venner et al. (2016)

2. Causes proximales: Effet Moran

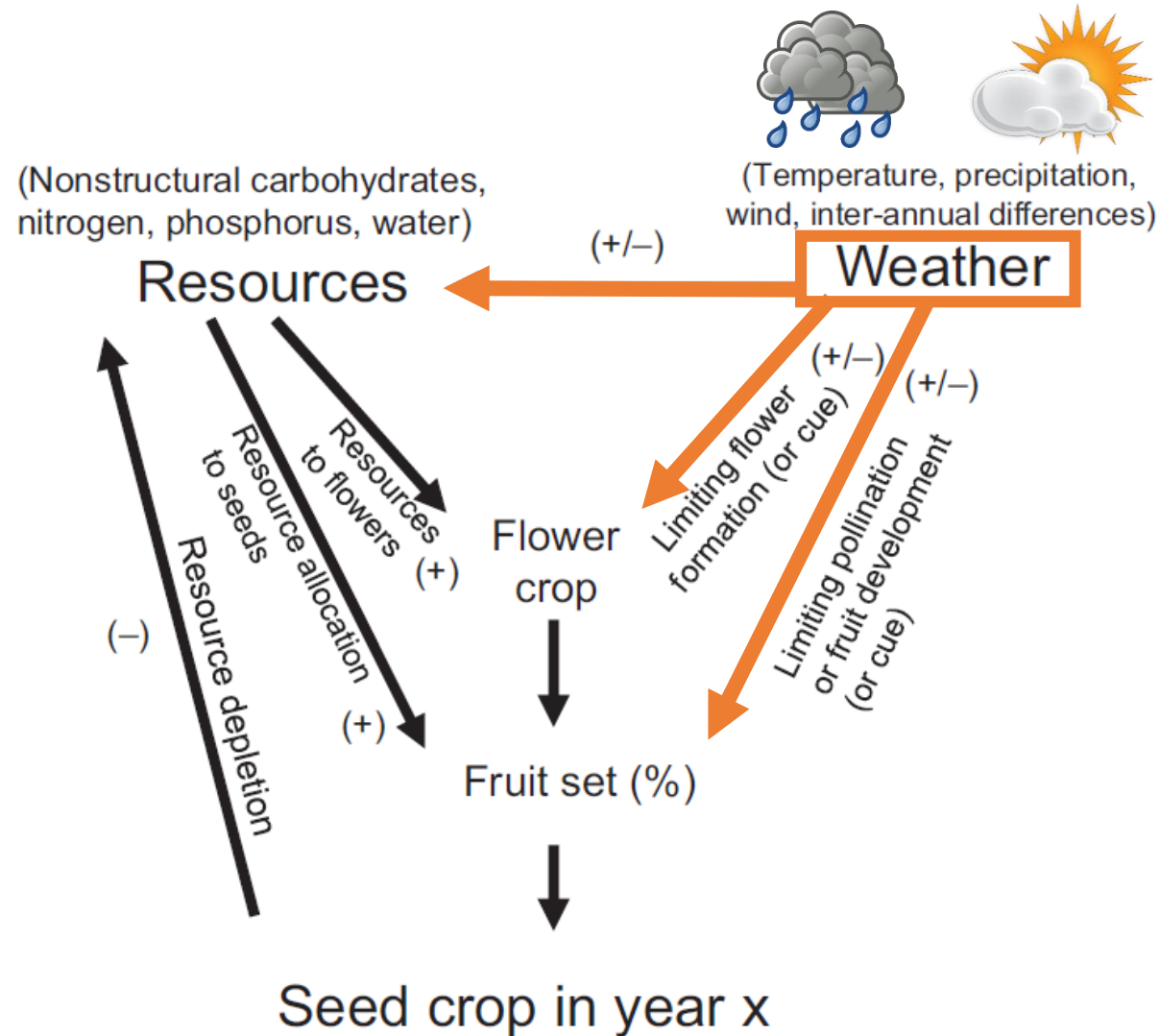
Variable climatique et
efficacité pollinique peuvent
expliquer la synchronie sur une
large échelle géographique



2. Causes proximales: Effet Moran

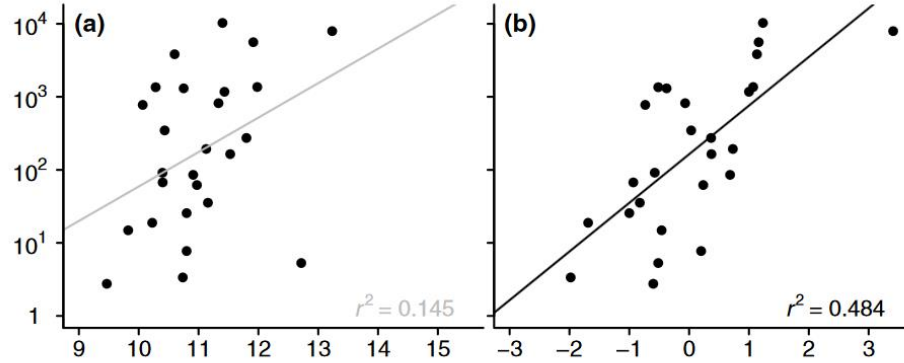


2.1. Causes proximales: Signal climatique

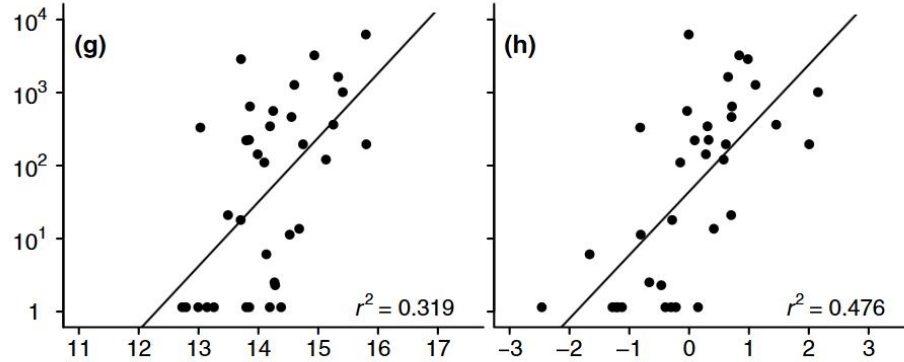


2.1. Causes proximales: Signal climatique

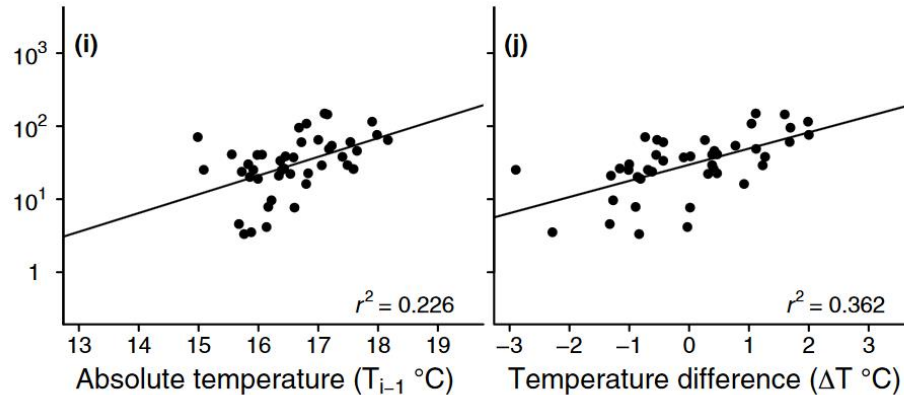
Chionochloa pallens



Nothofagus fusca



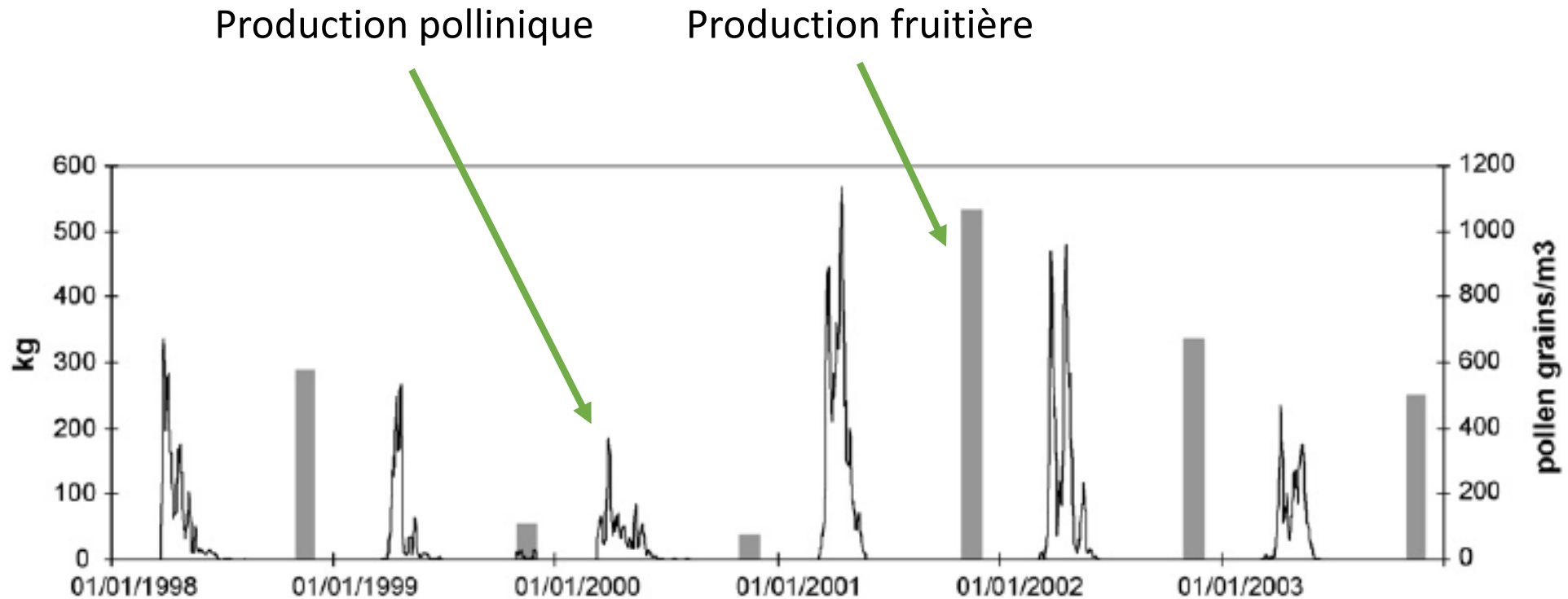
Elaeocarpus dentatus



Temperature differential cue:
 $\Delta T = T_n - T_{n-1}$

2.2. Causes proximales: **Signal pollinique**

Efficienc pollinique: La densité de production de pollen influe sur la synchronie et le CVi en cas de d'échec pollinique



2.3. Causes proximales: vers une réunification des théories

H1. Phenological synchrony hypothesis

H2. Aerial diffusion hypothesis

Micro-climate variability

Photoperiod sensitivity –
Genetic variability

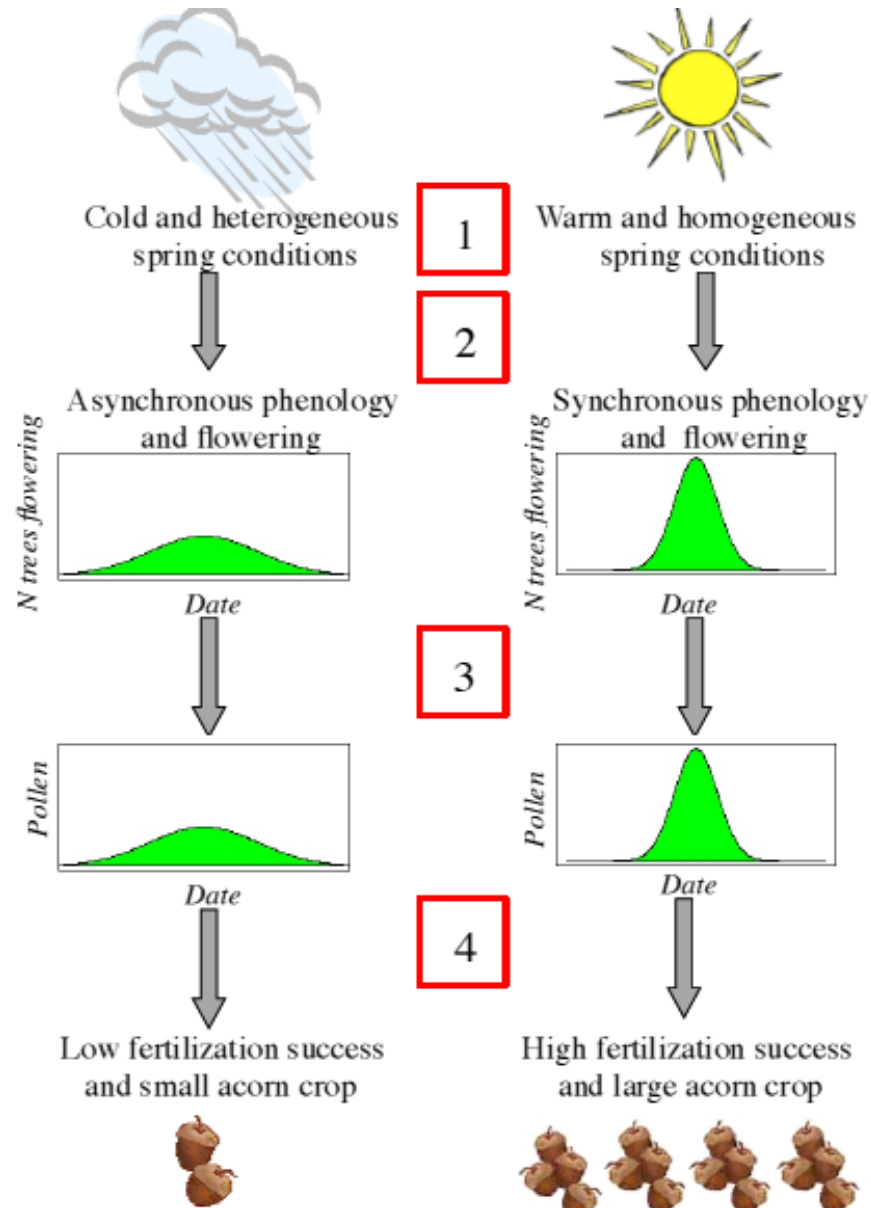
*Weather affect the diffusion of pollen
in the air (Schermer et al.
2020, 2019).*

*Microclimate heterogeneity affect the
phenology differently between trees
(Koenig et al. 2015).*

*High variability of photoperiod
sensitivity between trees affect the
phenology (Fu et al. 2019).*

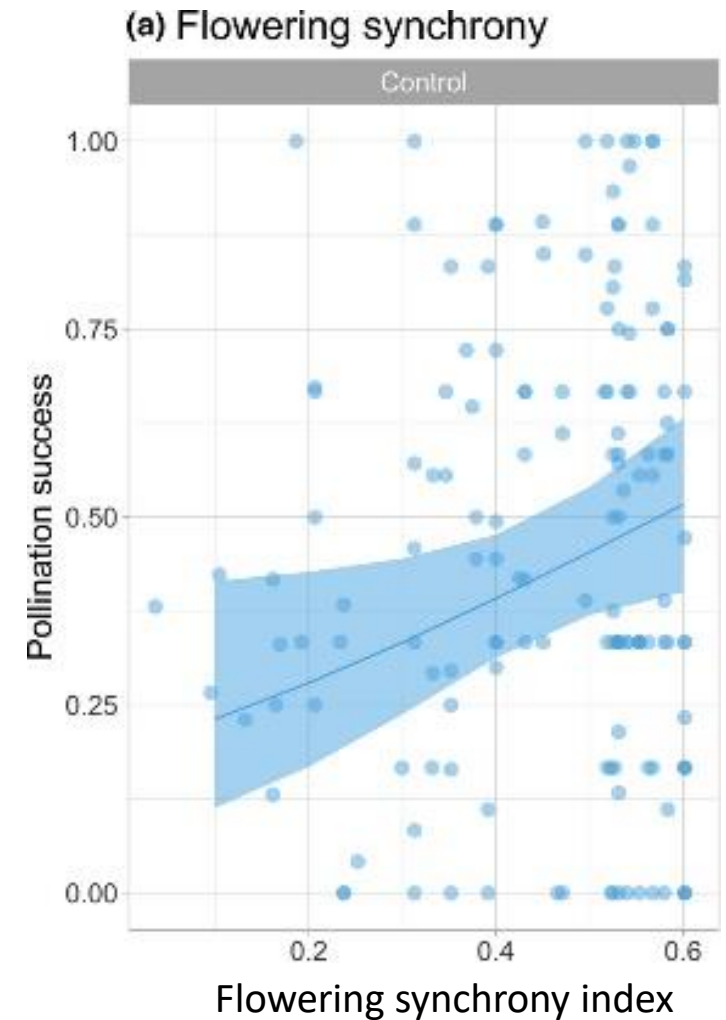
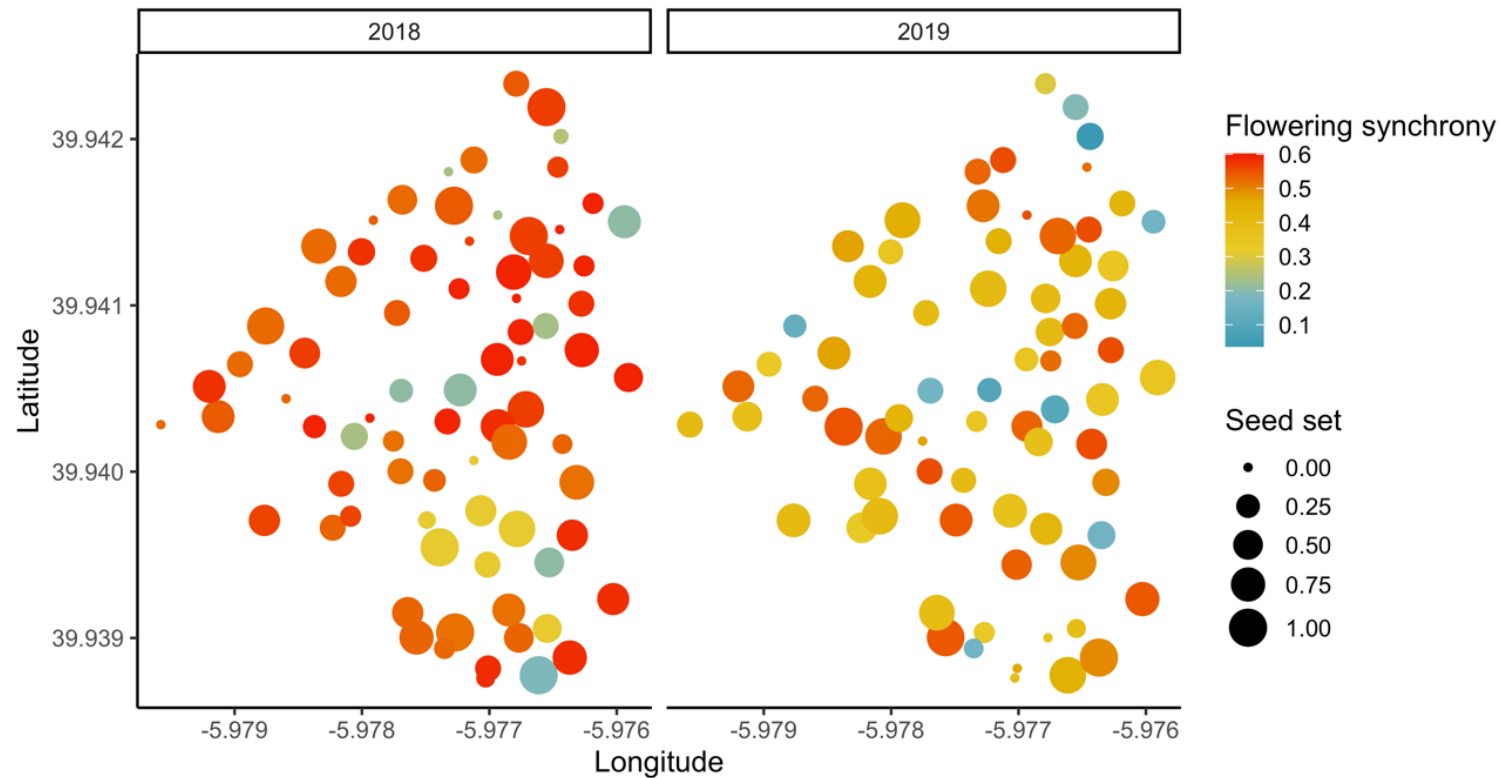
Pollination success

2.3. H1 : Phenological synchrony hypothesis



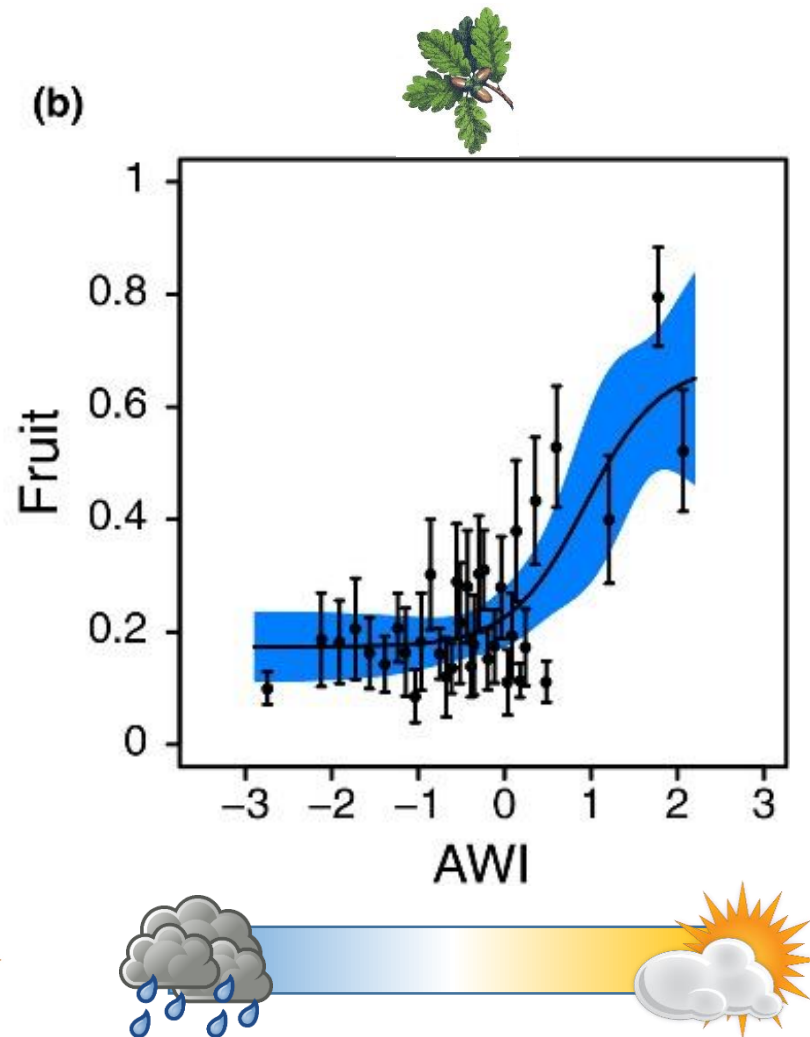
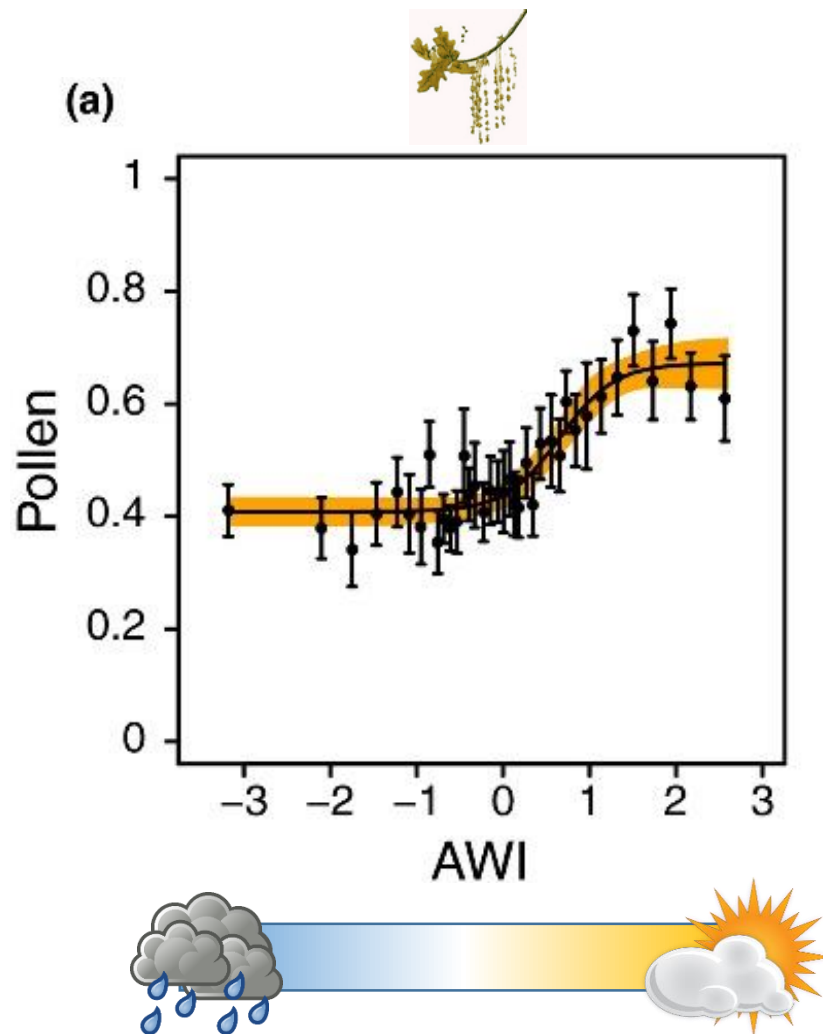
Modèle en série:
« Phenological synchrony hypothesis »
Koenig et al. (2015)

2.3. H1 : Phenological synchrony hypothesis

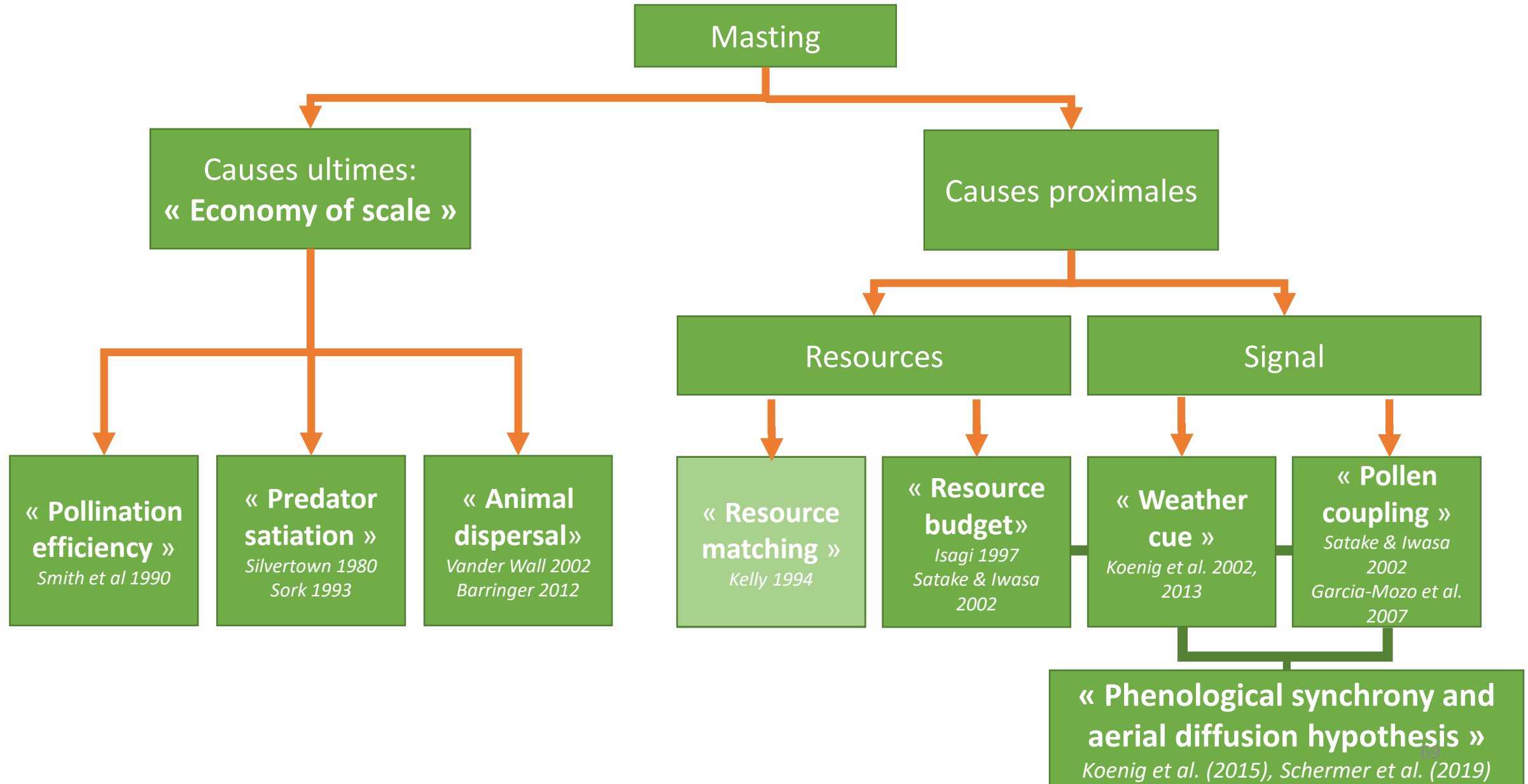


2.3. H2: Aerial diffusion hypothesis

Impact des variations climatiques sur l'efficacité pollinique et en conséquence sur la production de graines



Les théories explicatives du masting: en résumé



3.1. Causes proximales: Signal hormonal

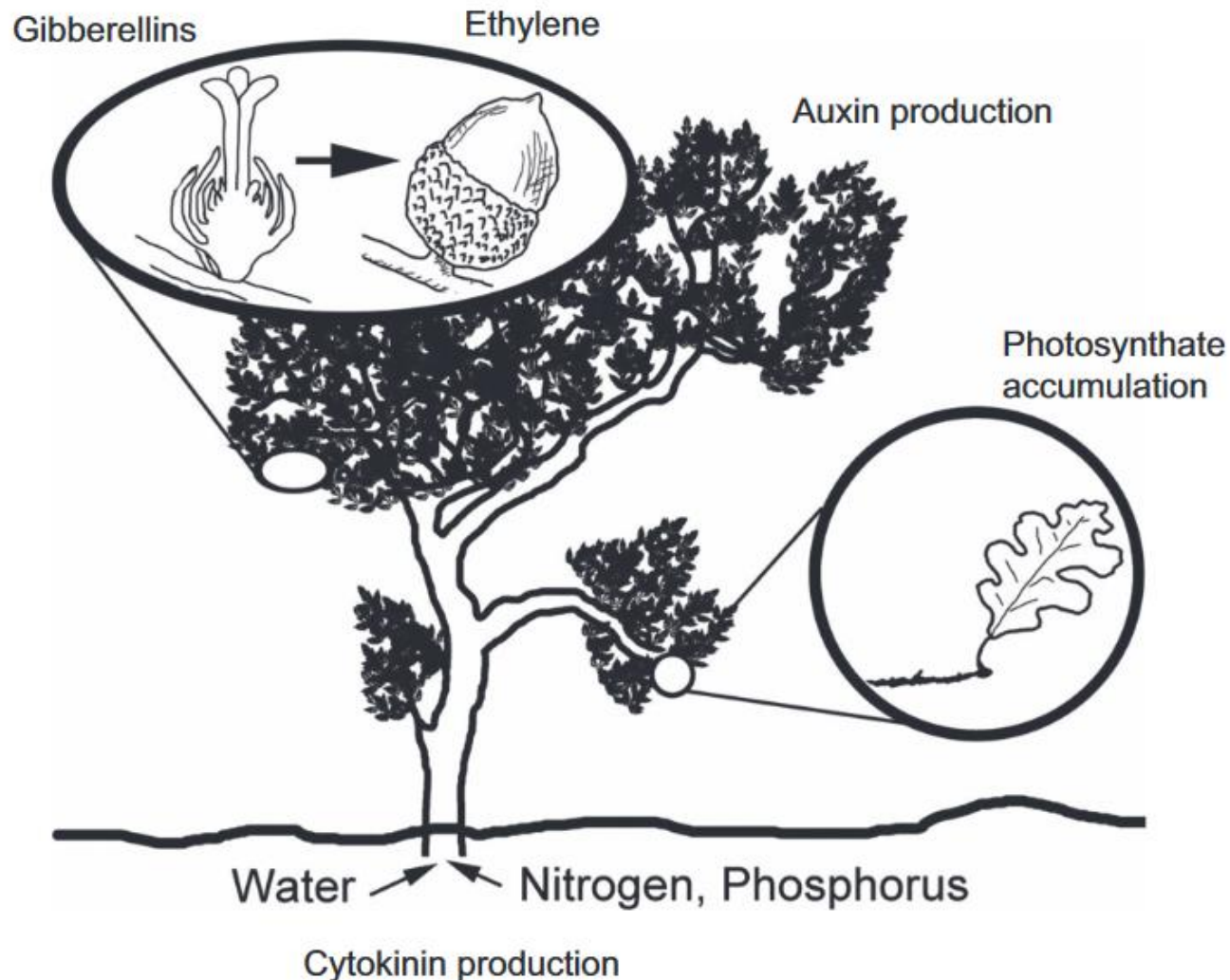


Table 6 The potential role of mobile signalling molecules in flower and seed set in masting plants

Signalling molecule	Putative role in flowering and seed set
Gibberellins (GAs)	Promote floral induction in <i>Arabidopsis</i> . Increase flowering in masting <i>Chionochloa</i> . Role in flower induction may be species-specific. Produced in leaves
Abscisic acid (ABA)	Is affected by carbohydrate concentrations, and implicated in resource allocation during reproduction
Ethylene (ETH)	Induces organ abortion, including flower and fruit abortion. A volatile signal produced and consumed endogenously within the fruit and flower
Cytokinins	Promote floral induction in <i>Sinapis</i> . Root-derived signal that is transported throughout aboveground plant tissue. May interact with other signals, such as TSF ('Twin Sister of FT')
FT and TSF proteins	Induce flowering in various plants. Lack of FT ('Flowering locus T') represses flowering in immature <i>Populus</i> trees. Produced in leaves and transported through phloem
Sugars	Act as mobile signals <i>per se</i> and also interact with other mobile signals such as FT and GA. Are in constant flux with metabolic demands and source–sink dynamics

3.2. Causes proximales: **Déterminisme génétique**

Détection de **QTL (Quantitative Trait Loci)** sur des traits caractéristiques du Masting : CV_i et Synchronie

Exemple du pommier (*Guitton et al. 2012*)

« Alternate-bearing » associé avec 4 régions génomiques contenant des gènes impliqués dans:

- Les hormones de la floraison
- La croissance des rameaux



3.2. Causes proximales: Déterminisme génétique



Fagus crenata

Floral pathway integrator:

- FLOWERING LOCUS T (FT)

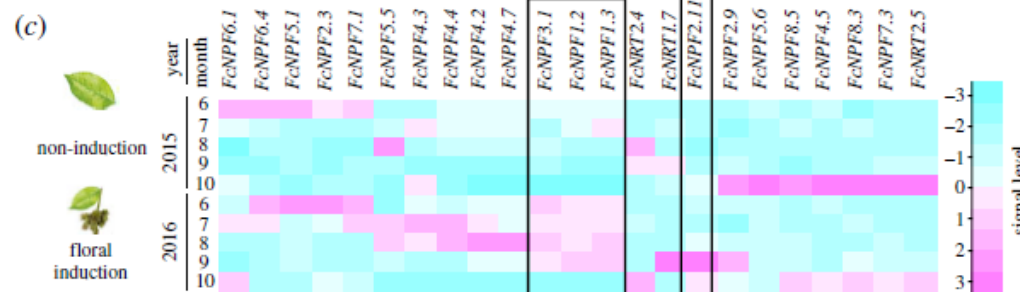
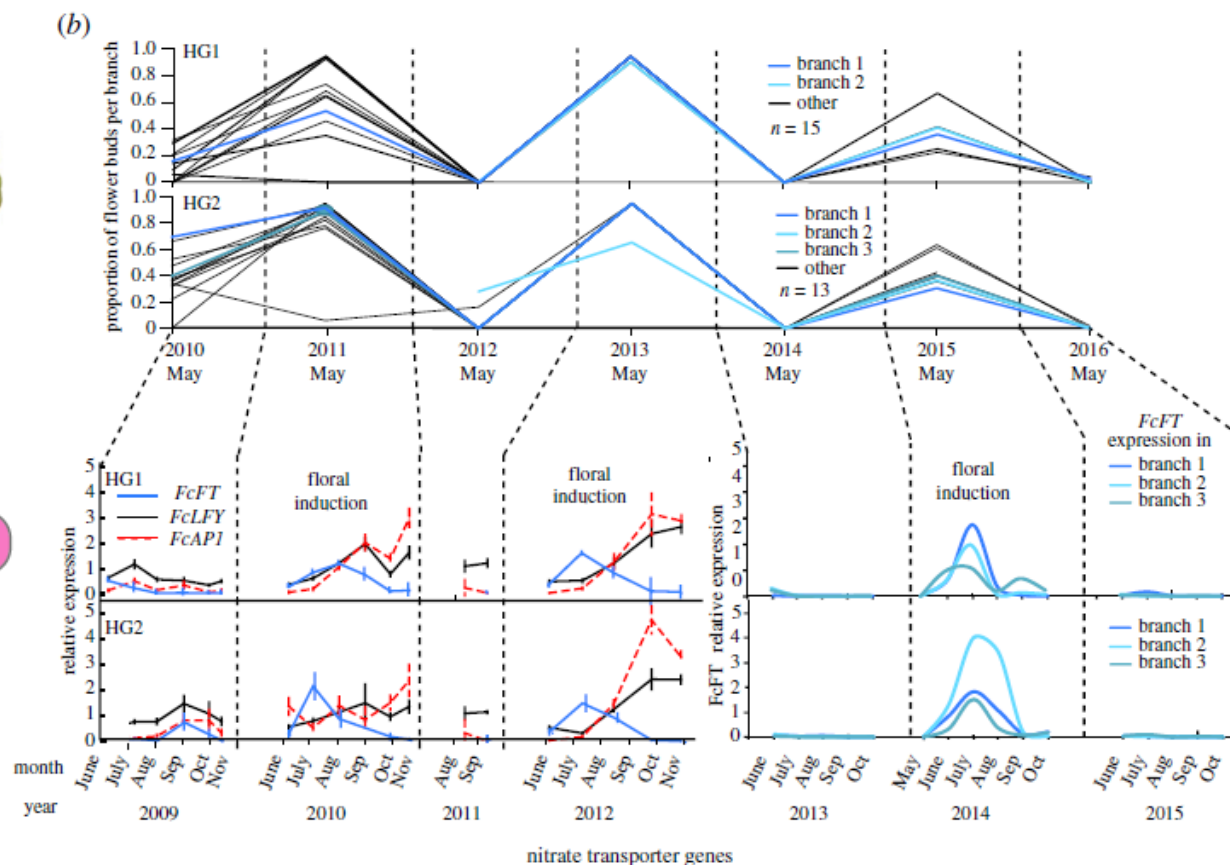
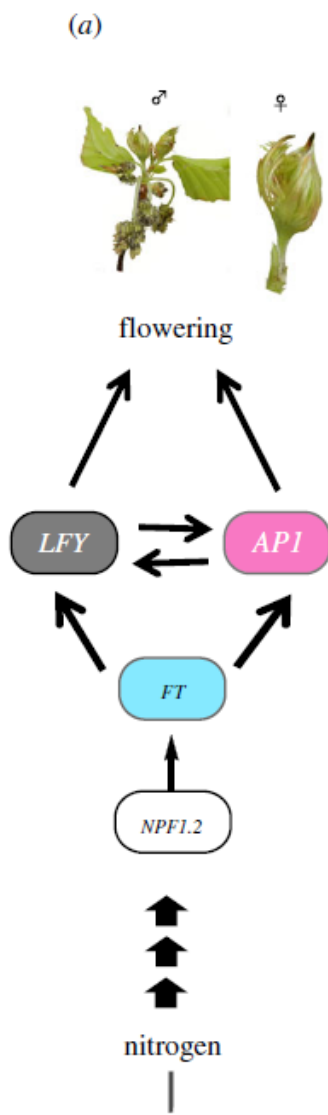
Genes promoting flower primordium identity:

- LEAFY (LFY)
- APETALA1(AP1)

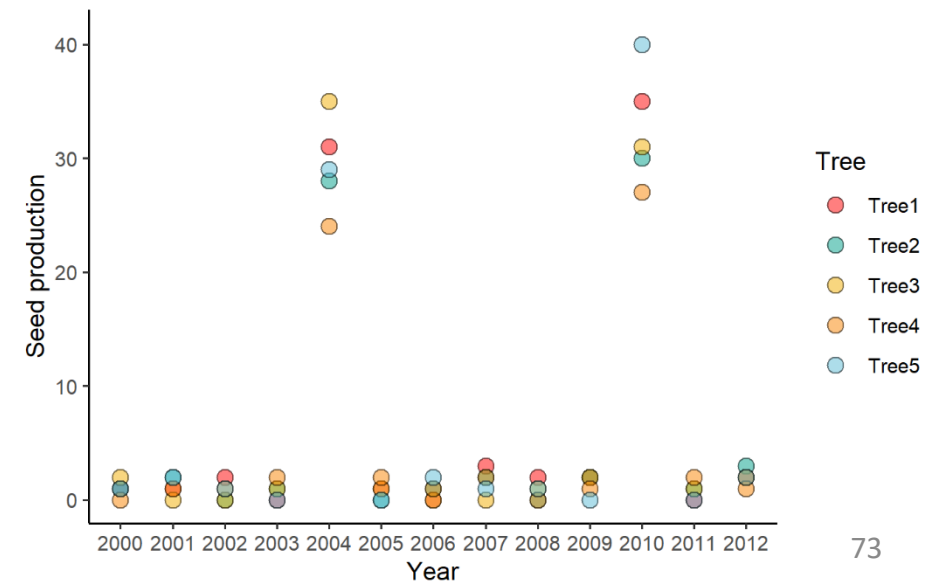
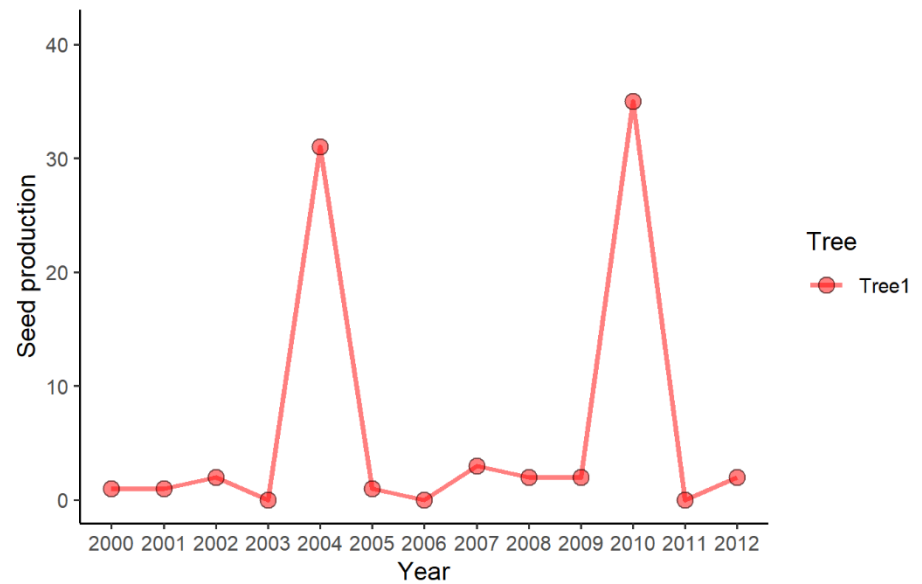
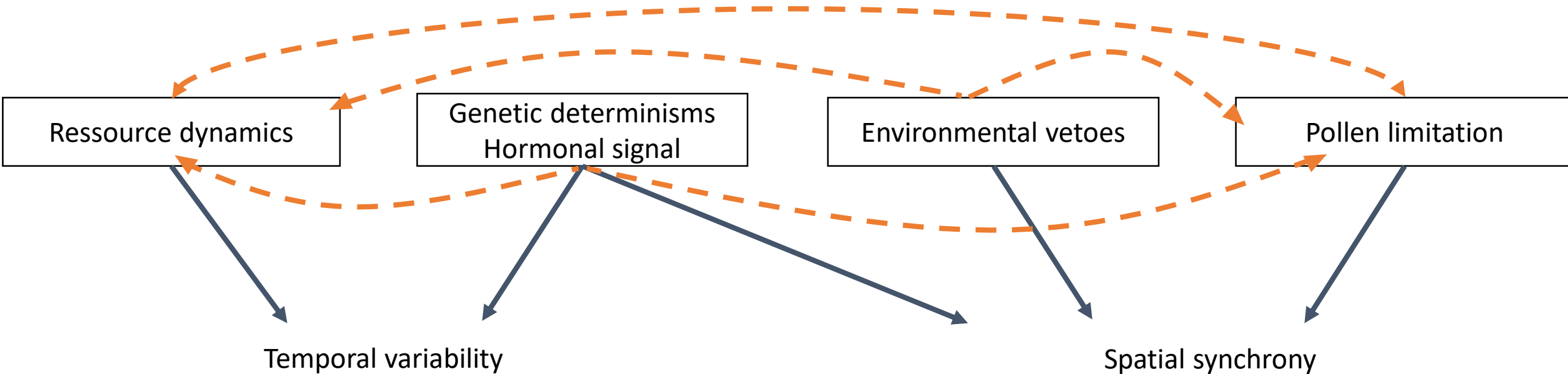
Nitrate transporter gene:

- (NPF1.2)

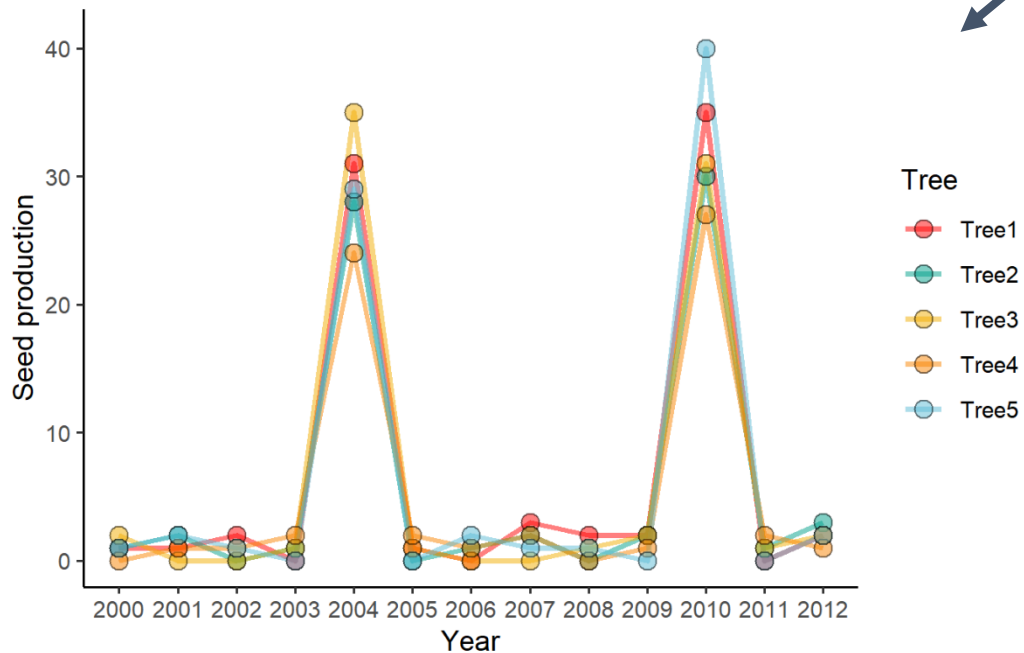
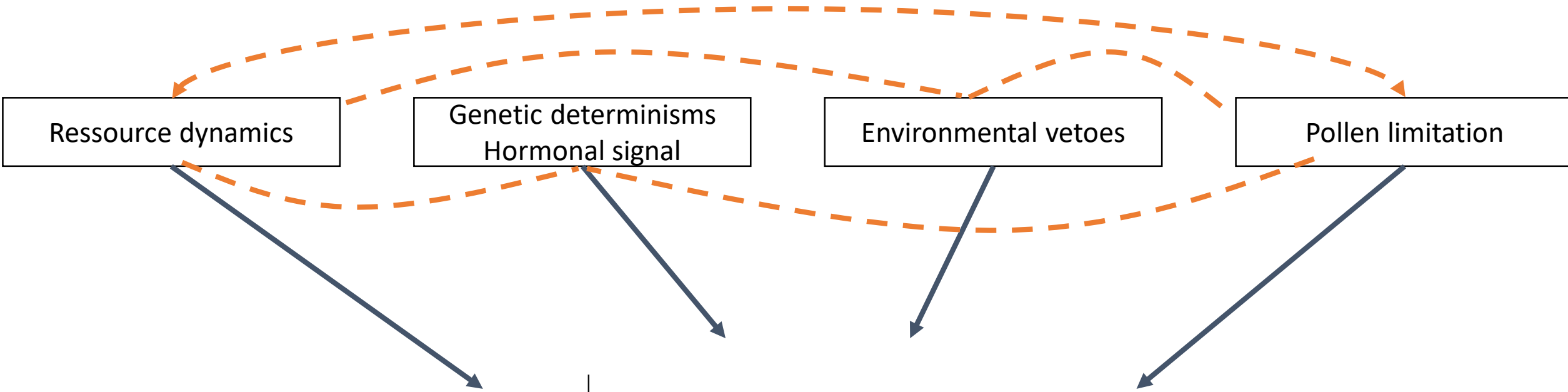
Satake & Kelly 2021



Les causes proximales: Summary



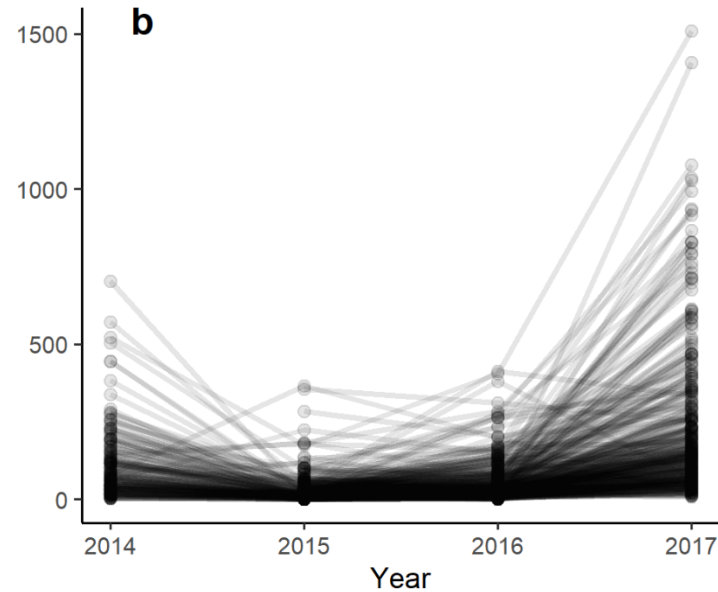
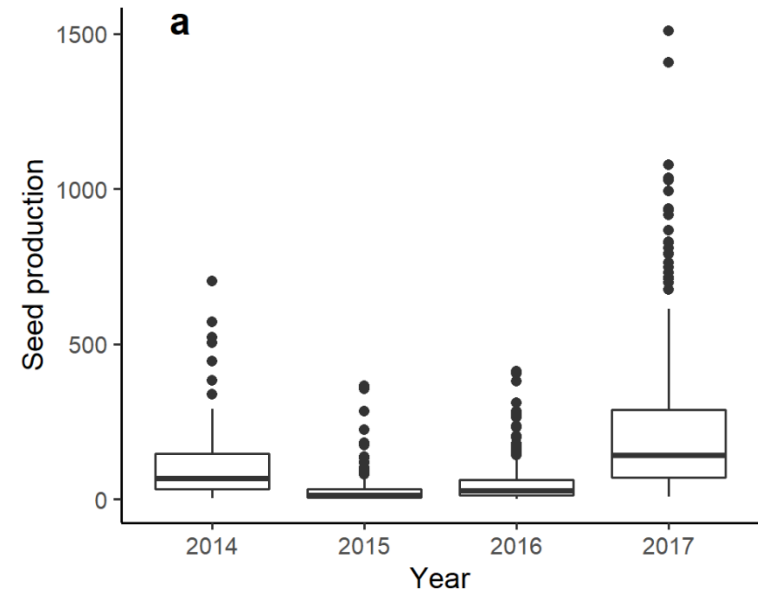
Les causes proximales: Summary



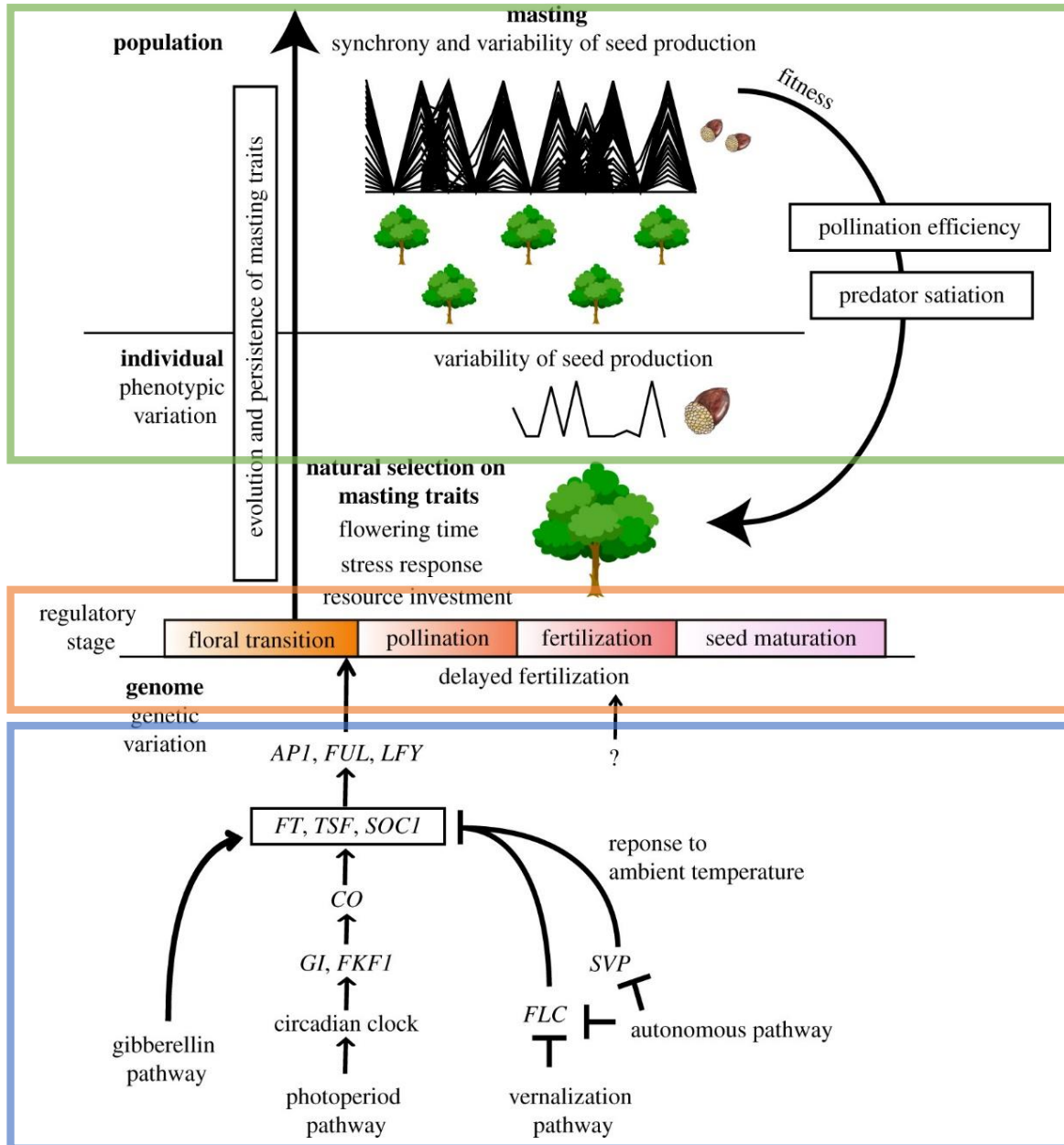
3.2. La masting peut-il être soumis à la sélection?

		Seed production			
		2014	2015	2016	2017
h^2_0		0.59	0.62	0.46	0.69

		Masting	
		CV_i	r_i
h^2_0		0.49	0.40



Comprendre les mécanismes pour étudier l'évolution du masting



1. Quels sont les traits clés qui régulent le masting?

2. Existe-il une évidence d'une régulation génétique?

3. Existe-il de la variabilité génétique et phénotypique des traits régulant le masting?

Current Biology

CellPress

Report

Climate Change Strengthens Selection for Mast Seeding in European Beech

Michał Bogdziewicz,^{1,2,8,*} Dave Kelly,³ Andrew J. Tanentzap,⁴ Peter A. Thomas,⁵ Jonathan G.A. Laguard,⁶ and Andrew Hacket-Pain⁷

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²CREAF, Universitat de Autònoma Barcelona, Cerdanyola del Valles, 08193 Catalonia, Spain

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⁴Ecosystems and Global Change Group, Department of Plant Sciences, University of Cambridge, Downing St., Cambridge CB2 3EA, UK

⁵School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK

⁶Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK

⁷Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool L69 7ZT, UK

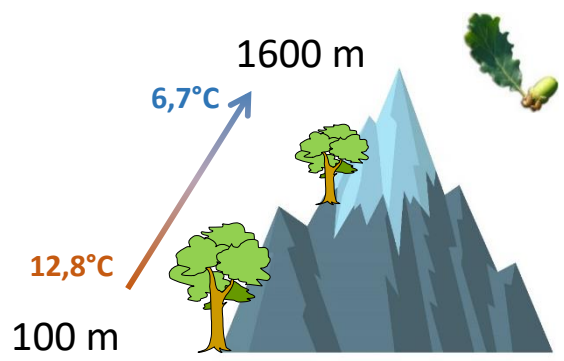
⁸Lead Contact

*Correspondence: michalbogdziewicz@gmail.com

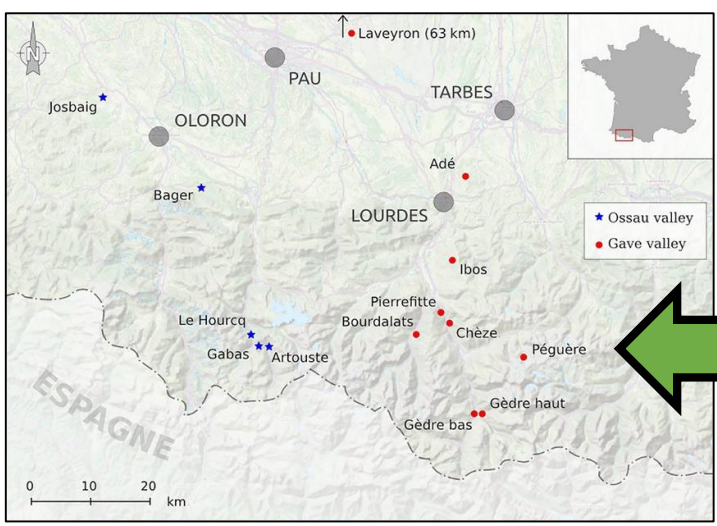
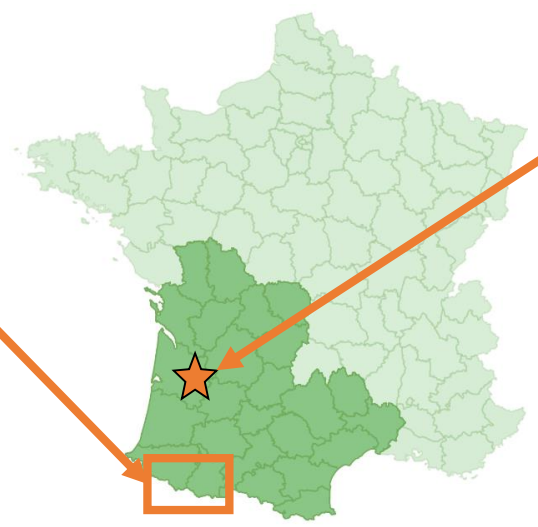
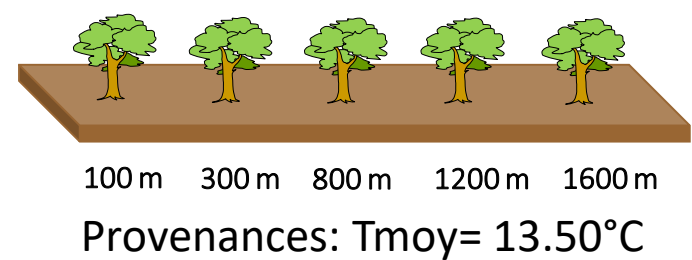
<https://doi.org/10.1016/j.cub.2020.06.056>

Perspectives: Variabilité de l'intensité du masting

In situ: Pyrenees



Common garden: Toulonne



- 2 vallées
- 10 stations
- Gradient d'altitude:
 - 100 m
 - 400 m
 - 800 m
 - 1200 m
 - 1600 m

In situ

Provenances



➔ Variabilité phénotypique (V_P)

➔ Variabilité génétique (V_G)

ISSN 0962-8436 | Volume 376 | Issue 1839 | 6 December 2021

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

BIOLOGICAL SCIENCES

The ecology and evolution of synchronized seed production in plants

Theme Issue compiled and edited by Mario B. Pesendorfer, Davide Ascoli, Michał Bogdziewicz, Andrew Hacket-Pain, Ian S. Pearse and Giorgio Vacchiano



THE
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SOCIETY
PUBLISHING

About this issue

Many long-lived plants show extraordinary year-to-year variation in seed production, ranging from bumper crops to years with crop failure. This phenomenon, known as masting or mast-seeding, occurs synchronously among trees of the same forest, among distant forests, and even across whole continents. Masting affects growth, survival, and regeneration of trees and forests, thus also driving evolutionary dynamics. Moreover, masting consequences cascade through ecosystems, affecting animal populations and disease dynamics, as well as subsistence ecosystem services from wild and cultivated crop plants.

In this theme issue, proximate and evolutionary mechanisms and functions of masting are explored from local to global scales. Masting forecasts, which constitute the next frontier in the field, will optimise the timing of conservation and land management efforts.

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Front image: Male and female cones of Norway spruce (*Picea abies*) during a mast year. Credit: Giorgio Vacchiano.

Introduction: The ecology and evolution of synchronized reproduction in long-lived plants
Mario B Pesendorfer, Davide Ascoli, Michał Bogdziewicz, Andrew Hacket-Pain, Ian S Pearse and Giorgio Vacchiano

A brief history of masting research
Walter D Koenig

Studying the genetic basis of masting
Akiko Satake and Dave Kelly

Delayed fertilization facilitates flowering time diversity in Fagaceae
Akiko Satake and Dave Kelly

By wind or wing: pollination syndromes and alternate bearing in horticultural systems
Gabriela Garcia, Bridget Re, Colin Orians and Elizabeth Crone

Mast seeding promotes evolution of scatter-hoarding
Rafal Zwolak, Dale Clement, Andrew Sih and Sebastian J Schreiber

Macroevolutionary consequences of mast seeding
Esther E Dale, Jessie J Foest, Andrew Hacket-Pain, Michał Bogdziewicz and Andrew J Tanentzap

Fire history and weather interact to determine extent and synchrony of mast-seeding in rhizomatous scrub oaks of Florida
Mario B Pesendorfer, Reed Bowman, Georg Gratzer, Shane Pruett, Angela Tringali and John W Fitzpatrick

Natural disturbances and masting: from mechanisms to fitness consequences
Giorgio Vacchiano, Mario B Pesendorfer, Marco Conedera, Georg Gratzer, Lorenzo Rossi and Davide Ascoli

An assessment of temporal variability in mast seeding of North American Pinaceae
Jalene M LaMontagne, Miranda D Redmond, Andreas P Wion and David F Greene

Modes of climate variability bridge proximate and evolutionary mechanisms of masting
Davide Ascoli, Andrew Hacket-Pain, Ian S Pearse, Giorgio Vacchiano, Susanna Corti and Paolo Davini

The effects of ENSO and the North American monsoon on mast seeding in two Rocky Mountain conifer species
Andreas P Wion, Ian S Pearse, Kyle C Rodman, Thomas T Veblen and Miranda D Redmond

Climate change and plant reproduction: trends and drivers of mast seeding change
Andrew Hacket-Pain and Michał Bogdziewicz

Understanding mast seeding for conservation and land management
Ian S Pearse, Andreas P Wion, Angela D Gonzalez and Mario B Pesendorfer



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