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**VULNÉRABILITÉ DES FORÊTS FACE AUX
PERTURBATIONS CLIMATIQUES, UNE
APPROCHE PAR SIMULATION
DÉMO-GÉNÉTIQUE POUR RAISONNER DES
STRATÉGIES DE GESTION ADAPTATIVE DU
CÈDRE ET DU SAPIN DOUGLAS**

Victor Fririon

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

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École doctorale GAIA

Unité de Recherche des Forêts Méditerranéennes (URFM – INRAE)

VULNÉRABILITÉ DES FORÊTS FACE AUX PERTURBATIONS CLIMATIQUES, UNE APPROCHE PAR SIMULATION DÉMO-GÉNÉTIQUE POUR RAISONNER DES STRATÉGIES DE GESTION ADAPTATIVE DU CÈDRE ET DU SAPIN DOUGLAS

Présentée par Victor FRIRION

Le 07 décembre 2022

Sous la direction de François LEFÈVRE et Hendrik DAVI

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Résumé

Face au changement climatique, se pose la question de la capacité intrinsèque naturelle des forêts à y faire face et des impacts positifs ou négatifs de la gestion sylvicole. Luberon2, un modèle Démographique Génétique individu-centré (DG-ABM) qui intègre des régimes de perturbation stochastiques a été développé pour apporter des réponses.

À partir du modèle Luberon2, deux plans de simulation sont analysés :

1. Dans les écosystèmes forestiers, la sélection naturelle dépend étroitement de la compétition interindividuelle qui se manifeste notamment par le processus d'auto-éclaircie, c'est-à-dire la suppression des plus petits arbres lorsque la densité est élevée. Nous montrons une augmentation rapide de la vigueur et des performances de croissance des peuplements monospécifiques de cèdre en réponse à un environnement social compétitif sélectif. Nous montrons également qu'une gestion intensive, i.e. nombreuses éclaircies systématiques, en réduisant la compétition, limite la capacité d'évolution des peuplements, fait aggravé en présence de perturbations naturelles non sélectives. Les taux d'évolution observés sont dans une gamme empirique réaliste, ce qui représente un élément fort de validation du modèle.

2. Une stratégie classique d'adaptation au changement climatique consiste à maintenir une faible densité d'arbres via une sylviculture intensive pour réduire le niveau de stress pendant les sécheresses et limiter ses impacts directs. Néanmoins, nous montrons que la sélection naturelle pour une moindre sensibilité a le potentiel d'induire une réponse positive rapide en termes de croissance et de survie appréciable dès la première génération, et qu'une intensification de la sylviculture réduit ce potentiel adaptatif chez des peuplements monospécifiques de sapin Douglas. Dès lors qu'il y a de la diversité génétique, c'est-à-dire le cas réaliste, nous montrons qu'une sylviculture moins intensive, visant à favoriser l'adaptation spontanée, représente la meilleure stratégie pour favoriser la productivité et abaisser la vulnérabilité. En particulier, le maintien d'un niveau élevé de stress à un stade de peuplement juvénile semble être une stratégie prometteuse pour favoriser l'acclimatation et l'adaptation précoce.

Le rôle de la diversité génétique et des processus évolutifs ainsi que l'impact de la gestion sont discutés en détail dans le cadre de diverses stratégies d'adaptation de la sylviculture au changement climatique et à la lumière de la large étude bibliographique effectuée sur les interactions entre perturbations, pratiques de gestion et diversité génétique.

Mots clés : Modèle démo-génétique - Adaptation génétique - Gestion forestière - *Pseudotsuga menziesii* - *Cedrus atlantica* - Régimes de perturbation - Changement climatique - Éco-évolution

Summary

Faced with climate change, the question arises of the intrinsic natural capacity of forests to cope with it and of the positive or negative impacts of forestry management. Luberon2, a Demo-Genetic individual-based model (DG-ABM) that integrates stochastic disturbance regimes has been developed to provide answers.

From the Luberon2 model, two simulation plans are analyzed:

1. In forest ecosystems, natural selection depends on inter-individual competition which is manifested in particular by self-thinning, i.e. the removal of the smallest trees when the density is high. We show a rapid increase in vigor and growth performance in monospecific cedar stand in response to a competitive and selective environment. We also show that intensive management, i.e. numerous systematic thinnings, limits the evolution of stands by reducing competition, which is aggravated in the presence of non-selective natural disturbances. The observed evolution rates are in a realistic empirical range, which represents a strong element of validation of the model.

2. A classic strategy for adapting to climate change is to maintain a low tree density through intensive silviculture to reduce the stress level during droughts and limit the direct impacts. Nevertheless, we show that natural selection for lower sensitivity has the potential to induce a rapid positive response in terms of growth and survival visible from the first generation, and that intensification of silviculture reduces this adaptive potential in monospecific Douglas-fir stands. When there is genetic diversity, i.e. the realistic case, we show that less intensive silviculture, aiming at promoting spontaneous adaptation, represents the best strategy for promoting productivity and lowering vulnerability. In particular, maintaining a high stress level at a juvenile stand stage appears to be a promising strategy to promote early acclimatization and adaptation.

The role of genetic diversity and evolutionary processes as well as the impact of management are discussed in detail in the context of various adaptation strategies of forestry to climate change and in the light of the extensive literature review carried out on the interactions between disturbances, management practices and genetic diversity.

Keywords: Demo-genetic model - Genetic adaptation - Forest management - *Pseudotsuga menziesii* - *Cedrus atlantica* - Disturbance regimes - Climate change - Eco-evolution

SOMMAIRE

Introduction	11
I - Contexte sociétal : vers un enrichissement du dialogue entre chercheurs et gestionnaires	14
1. Les modèles au service de la gestion	14
2. Face au changement global, un intérêt croissant pour les modèles basés sur les processus	15
3. Vers le développement de modèles innovants qui intègrent l'évolution rapide	16
II - Contexte scientifique : revue de la littérature des interactions entre perturbations, diversité génétique et pratiques de gestion	18
1. Depuis la perturbation jusqu'à son régime d'intensité	18
1.1. Définir une perturbation : derrière une question sémantique, de vrais choix	18
1.2. Intégrer les perturbations dans l'espace et dans le temps : régime de perturbation	20
1.3. Intégrer la relation entre intensité et impact : régime d'impact	21
2. Altération des régimes de perturbations : la vulnérabilité des écosystèmes forestiers	23
2.1. Changement global : altération des régimes de perturbation en cours	23
2.2. Notion de risque d'effondrement	24
2.3. L'enjeu de la biodiversité : cas de la diversité génétique	25
2.4. Vers un risque d'effondrement grandissant	26
3. Le cadre de l'approche risque et multirisque	28
3.1. Le risque, un concept multi-facette	28
3.2. Introduction à la gestion des risques en forêt	30
4. Gestion et pratiques sylvicoles : mieux intégrer la gestion des risques	32
4.1. La gestion pour agir sur l'aléa et la sensibilité	32
4.2. Le choix de la ressource génétique pour contrôler la sensibilité	34
4.3. La capacité d'adaptation vue comme un facteur de moindre vulnérabilité	35
III - Objectifs et démarche générale de l'étude	39
1. Objectifs de l'étude	39
2. Description générale de la démarche	41

IV - Le choix d'une approche par modélisation Démo-Génétique	44
1. L'approche par modélisation Démo-Génétique : un choix adapté aux questions de l'étude	44
2. Article 1 (publié) . Importance of interindividual interactions in eco-evolutionary dynamics: the rise of demo-genetic agent-based models	46
3. Luberon2, un modèle démo-génétique pour l'étude des interactions entre la gestion et les processus évolutifs en forêt	83
V - Luberon2 comme preuve de concept de l'approche par modélisation démo-génétique en forêt	86
1. La question de la validation du couplages démo-génétiques de Luberon2	86
2. Article 2 (en cours de finalisation) . A demo-genetic model shows that non-selective silviculture and disturbances affect natural selection in tree populations	88
3. Ajouter du sélectif aux perturbations et aux interventions sylvicoles	118
3.1. Les perturbations, des moteurs de la sélection	118
3.2. Éclaircir par le bas pour suivre la direction du gradient de sélection	118
VI - Conceptualiser et formaliser un régime d'impact de type sécheresse pour l'intégration dans un modèle DG-ABM	121
1. Les sécheresses : de l'aléa jusqu'aux impacts démographiques	121
1.1. De la physiologie...	121
1.2. ... à la démographie	122
2. Article 3 (publié) . Within and between population phenotypic variation in growth vigor and sensitivity to drought stress in five temperate tree species	124
3. Vers l'estimation des paramètres génétiques de sensibilité pour la suite de l'étude	166
VII - Evaluation Démo-Génétique des stratégies d'adaptation de la sylviculture du sapin Douglas aux sécheresses	169
1. Développement de Luberon2 dans le cadre de mes travaux	169
1.1. Implémentation du sapin Douglas	169
1.2. Implémentation du régime d'impact sécheresse	169
2. Article 4 (en cours de finalisation) . Silviculture as an eco-evolutionary lever for risk management under drought disturbance regime	171
VIII - Discussion générale	206
1. Synthèse des principaux résultats scientifiques	206
1.1. Résumé des travaux réalisés	206

1.2. Confrontation de l'étude avec la littérature scientifique	209
1.2.1. Sur les capacités de microévolution des peuplements forestiers	209
1.2.2. Sur les conséquences démo-génétiques de la gestion des peuplements	210
2. Analyse critique de l'étude	212
2.1. Pertinence des sorties du modèle Luberon2	212
2.2. Considérations dans le cadre de l'approche multirisques	213
3. Perspectives	214
3.1. Luberon2, un outil pour les gestionnaires	214
3.2. Vers des régimes de perturbation non stationnaires	215
3.3. Stratégie d'enrichissement génétique et mélange de populations	215
Conclusion générale	218
Références bibliographiques du corps de texte	221
Annexe 1 : annexes des articles	240
Article 1. Figures et Tableaux supplémentaires (S1 à S3)	240
Article 2. Échelles spatiales et temporelles dans Luberon2 (1), Conséquences du choix de la taille des pixels (2), Fonctions de croissance et de fécondité de Luberon2 (3) et Figures supplémentaires (4)	243
Article 3. Données et Figures supplémentaires	258
Article 4. Calibration de trois distributions gamma du niveau de stress (A) et Figures supplémentaires (B)	265
Annexe 2 : ressources pour le développement de Luberon2	270
Outil de travail pour implémenter le sapin Douglas (depuis Gymnos) et le formalisme de régimes d'impact sécheresse dans Luberon2	270
Récapitulatif des principaux paramètres pouvant varier d'une espèce à l'autre dans Luberon2	277

Introduction

Les perturbations sont omniprésentes, inévitables et affectent tous les niveaux d'organisation biologique. Les écosystèmes sont influencés par des perturbations de toutes sortes, telles que des incendies, des tempêtes, des glissements de terrain, des inondations, des sécheresses, des épidémies d'agents pathogènes, etc.

Le changement climatique contribue aujourd'hui à altérer profondément les régimes de perturbation, ce qui impacte la capacité des écosystèmes à fournir des services écosystémiques et induit un risque de dépasser leur résilience écologique.

La vulnérabilité à de telles altérations est complexe et multifactorielle. Localement, elle dépend en particulier (i) de facteurs de sensibilité prédisposant à atteindre un certain niveau de dommages et (ii) de la capacité des populations à s'adapter aux changements environnementaux.

En particulier pour les organismes à longue durée de vie comme les arbres, la capacité intrinsèque des populations à faire face naturellement est sujet à débat. Néanmoins, un nombre croissant d'études suggèrent qu'une évolution génétique rapide peut se produire et alimenter un changement adaptatif appréciable sur quelques générations seulement.

Dans les populations exploitées comme les forêts, les interventions humaines modifient l'ensemble des facteurs de vulnérabilité (sensibilité et capacité d'adaptation). L'impact global des pratiques de gestion, positif ou négatif, est complexe à évaluer et, dans des objectifs d'adaptation, le choix de stratégies d'interventions, par exemple pour réduire le stress, ou de non intervention, pour favoriser la sélection naturelle, est sujet à débat. Il est pourtant indispensable de comprendre dès maintenant les impacts à court et à long terme pour évaluer et mettre en place des stratégies pérennes adaptées.

Dans cette thèse, la construction d'un modèle mécaniste démo-génétique individuel centré, reproduisant les impacts observés de la sécheresse sur la croissance, a permis de simuler les effets d'interaction entre perturbations climatiques, processus adaptatifs et gestion sur la croissance, la démographie et la diversité génétique des peuplements. La compréhension de ces effets et leur évaluation quantitative ont apporté un nouveau regard

sur les stratégies de gestion des écosystèmes forestiers pour la conservation durable de la nature et des besoins humains auxquels elle répond.

I - Contexte sociétal : vers un enrichissement du dialogue entre chercheurs et gestionnaires

La recherche s'intéresse depuis longtemps à la prédiction et la compréhension de l'évolution des peuplements forestiers, et s'attache à mettre au point des outils pour aider les gestionnaires dans l'aménagement et la gestion des forêts (Pardé & Bouchon, 1988). Compte tenu de la complexité de la dynamique des écosystèmes forestiers, les modèles sont particulièrement utiles pour (i) comprendre et maîtriser cette complexité et (ii) mettre les connaissances scientifiques au service de la gestion des écosystèmes (Bunnell & Boyland, 2003).

1. Les modèles au service de la gestion

Les premiers de ces outils sont les tables de production. Ce sont des tableaux qui permettent de prédire quantitativement l'évolution d'un peuplement régulier, pour certains scénarios sylvicoles classiques en fonction de la fertilité du lieu. La conception de ces tables de production a été rendue possible par l'observation à long terme de l'évolution de peuplements de référence. Ces premiers outils présentent deux inconvénients majeurs (Houllier et al., 1991) : ils se limitent à la prédiction de l'évolution moyenne des peuplements, et surtout, ils ne permettent pas de simuler différents types de sylviculture, et donc il était impossible de tester de nouveaux scénarios.

Lorsque l'avancée informatique l'a rendu possible, le développement de modèles empiriques, plus complexes, supportés informatiquement a été rapidement identifié comme le meilleur moyen de prendre en compte et d'évaluer la grande diversité des peuplements existant et des scénarios sylvicoles envisageables. Les modélisateurs forestiers ont alors développé un grand nombre de modèles empiriques pour comprendre et prédire l'évolution des arbres et des peuplements (Goreaud et al., 2005). Par exemple, en ce qui concerne la prédiction de la croissance des arbres, on peut distinguer, selon le niveau de détail souhaité ou nécessaire pour traiter une problématique donnée, des modèles à l'échelle du peuplement, qui considèrent uniquement l'évolution des caractéristiques moyennes du peuplement, des modèles de distribution, qui considèrent l'évolution du nombre d'arbres

dans différentes classes de diamètre et des modèles individus centrés, qui simulent l'évolution de chaque arbre individuellement. Ces modèles intègrent généralement d'autres processus démographiques tels que la mortalité occasionnée par la concurrence entre arbres, c'est-à-dire le phénomène d'auto-éclaircie, et la régénération.

2. Face au changement global, un intérêt croissant pour les modèles basés sur les processus

Malgré leurs capacités de prédiction actuelles, ces modèles empiriques souffrent d'une série de lacunes. Premièrement, ces modèles statistiques sont basés sur des enregistrements de croissance passés. Or, les changements climatiques ont le potentiel d'invalider rapidement les niveaux de référence historiques en modifiant les principaux moteurs des régimes de perturbation (Seidl et al., 2011). Ces modèles manquent donc de la flexibilité nécessaire pour tenir compte des changements des conditions de croissance, de mortalité et de reproduction. Deuxièmement, leur application repose sur le concept circulaire d'un indice de fertilité site-spécifique dans lequel le potentiel de croissance est défini à partir de la taille des arbres sur ce site à un certain âge, excluant ainsi les estimations de la productivité des sites récemment perturbées ou dont les régimes de perturbation sont en cours d'altération (Johnsen et al., 2001). Certains modèles permettent néanmoins une plus grande flexibilité de prédiction en intégrant un effet date, pour prendre en compte les changements de productivité (Dhote et al., 2007).

Les modèles basés sur les processus (PBM), c'est-à-dire les modèles qui caractérisent la dynamique d'un système à travers la description explicite de ses mécanismes internes, ont alors suscité un intérêt croissant, compte tenu de leur plus grande flexibilité et de leur potentiel d'application dans des environnements changeants (Härkönen et al., 2019 ; Battaglia & Sands, 1998). Trois types de modèles basés sur les processus sont traditionnellement utilisés pour prédire la réponse des populations d'arbres forestiers au changement global (Oddou-Muratorio et al., 2020) : (1) les modèles écophysologiques, qui simulent les flux de carbone et d'eau dans les écosystèmes forestiers en intégrant explicitement les effets du climat et du CO₂, (2) les modèles de dynamique forestière qui simulent les successions forestières en liant explicitement les processus de mortalité, de

croissance et de régénération et (3) les modèles de dynamique évolutive, qui simulent la variation et l'évolution des traits adaptatifs en tenant explicitement compte des règles de sélection, de mutation, de flux génétique et d'hérédité.

3. Vers le développement de modèles innovants qui intègrent l'évolution rapide

Le contexte actuel de changement climatique rapide remet en question les frontières entre les processus écophysologiques, démographiques et évolutifs alors qu'un nombre croissant d'études suggèrent que, lorsque la sélection est forte (compétition et altération rapide des régimes de perturbations par exemple), une évolution génétique rapide peut se produire et alimenter un changement adaptatif appréciable à l'échelle de quelques générations seulement (Pelletier et al., 2007, 2009). Notamment, les écologistes évolutionnistes s'aperçoivent que de nouvelles perspectives sur la dynamique évolutive peuvent être obtenues en intégrant plus de détails sur les processus démographiques, le contexte environnemental et leurs interactions dans les modèles de génétique des populations et de génétique quantitative (Hanski 2012 ; Hendry 2016). En parallèle, les gestionnaires forestiers ont commencé à intégrer les processus évolutifs dans leur réflexion lors des interventions et traitements sylvicoles, mais les outils mis à leur disposition ne permettent pas de quantifier l'impact de ces pratiques sur le potentiel adaptatif des peuplement forestiers (Legay et al., 2015). Dans ce contexte, l'intégration de processus écophysologiques, démographiques et évolutifs dans de nouveaux types de PBM, tels que les modèles démo-génétiques, semble être le choix le plus approprié pour raisonner sur des échelles de temps écologiques (Oddou-Muratorio et al., 2020).

II - Contexte scientifique : revue de la littérature des interactions entre perturbations, diversité génétique et pratiques de gestion

L'objectif de ce chapitre consiste à contextualiser l'ensemble de ma thèse en abordant le concept de perturbation dans le contexte du changement global et dans le cadre général d'une approche de gestion du risque en termes de risques démographiques et génétiques.

1. Depuis la perturbation jusqu'à son régime d'intensité

1.1. Définir une perturbation : derrière une question sémantique, de vrais choix

Alors que l'intérêt pour l'écologie des perturbations explose depuis les années 1970, la façon de définir une perturbation a été longuement discutée dans la littérature. En particulier, il existe un débat consistant à considérer ou non les interventions de gestion comme des perturbations. Dans le cadre de mes travaux, perturbation et intervention de gestion seront deux concepts distincts. Nous retiendrons une définition absolue de perturbation comme proposée par White & Pickett (1985) : la perturbation est un événement discret dans le temps qui modifie l'état des variables structurelles et physiques de l'écosystème, ces changements influençant également les fonctions et les processus de l'écosystème. Grime (1979) a proposé une approche simple et facilement mesurable de cette définition : une perturbation est un événement conduisant à une destruction de biomasse. Ainsi, les sécheresses estivales, les incendies dans les prairies ou les chutes d'arbres dans les forêts anciennes, bien qu'indissociables de la dynamique de l'écosystème, sont considérés comme des perturbations ; la perturbation étant une composante majeure et déterminante de l'écosystème. En outre, la réduction de croissance liée à une sécheresse par exemple, peut également être considérée comme une destruction de biomasse, potentielle cette fois (voir Lloret et al., 2011). Avec cette approche, une nouvelle question émerge donc : Quelle quantité de changements doit se produire pour utiliser le terme de perturbation ? La réponse à cette question dépend des propriétés intrinsèques de l'écosystème considéré.

En effet, la notion de perturbation n'est pas parfaitement binaire comme précédemment supposé : dans de nombreux cas, lorsqu'un facteur de stress est récurrent et indissociable de la dynamique du système, tel que le déficit hydrique estival ou la pression parasitaire, les valeurs d'intensité de ce facteur sont continues, un événement particulièrement extrême prenant naturellement sa place dans les valeurs extrêmes d'une distribution de probabilité continue (Kwon & Hyun Sung, 2019 ; Stagge et al., 2015). Notons ici que l'intensité désigne une mesure intrinsèque à la perturbation, indépendamment de ses effets, tels que le déficit hydrique lors d'une sécheresse, la vitesse des rafales de vent lors d'une tempête ou encore la densité des ravageurs lors d'une épidémie. La notion de perturbation (sécheresses, épidémies parasitaires, canicule, etc.) semble alors prendre sens lorsque les dommages engendrés par le facteur de stress sont jugés particulièrement préjudiciables au système (White & Pickett, 1985). La question se pose donc de savoir comment séparer objectivement ce qui est à considérer comme une perturbation de ce qui n'en est pas une pour ces pressions de nature graduelle. Des seuils statistiques (Szinell et al., 1998) ou des seuils fonctionnels basés sur la physiologie de l'espèce étudiée (Anderegg et al., 2015) peuvent être utilisés pour répondre à cette problématique et déterminer à partir de quelle valeur d'intensité le facteur de stress impose un risque significatif au système (Choat, 2013). Toutefois, s'il est facile de trancher entre perturbation ou simple stress à chacun des extrêmes de la distribution des valeurs d'intensité, l'emploi de seuils pour soutenir la définition de perturbation ne permet pas de penser correctement le passage de l'un à l'autre, et il serait préférable d'appliquer le principe de logique floue pour lequel tout état, plutôt que d'être vrai ou faux, est un réel compris entre 0 et 1. Dans un tel questionnement purement sémantique, il semble difficile de ne pas faire intervenir une part de subjectivité : nos attentes. Ainsi, la notion de risque, qui sera développée plus amplement par la suite, suppose une évaluation relative qui dépend des services écosystémiques rendus (production, régulation, etc.), de leur vulnérabilité aux aléas ainsi que de nos objectifs et besoins en termes de hiérarchisation et d'état fonctionnel de ces services.

L'ampleur d'une perturbation dépend de son intensité mais également de son étendue et de son patron spatial. On peut distinguer (1) les perturbations diffuses, c'est-à-dire celles pour lesquelles les zones concernées par la perturbation sont relativement petites et réparties au sein d'une aire plus large, c'est le cas lorsque, pendant une épidémie, un

pathogène s'attaque préférentiellement aux arbres déjà affaiblis ou à une essence spécifique en forêt mélangée, et (2) les perturbations discrètes, c'est-à-dire celles dans lesquelles la perturbation est agrégée en une grande aire relativement homogène, par exemple lors d'une sécheresse affecte tous les arbres d'un peuplement (White & Jentsch, 2001). L'ampleur apparente de la perturbation peut être la même dans ces deux cas (par exemple, une perte identique de surface foliaire à l'échelle du peuplement) sans pour autant représenter le même enjeu. Cependant, les perturbations discrètes et diffuses ne peuvent être définies que par référence à l'échelle. En effet, à une échelle spatiale plus fine, les perturbations diffuses sont constituées de zones de perturbations discrètes. De même, à de grandes échelles spatiales, des perturbations discrètes peuvent devenir diffuses.

1.2. Intégrer les perturbations dans l'espace et dans le temps : régime de perturbation

Une perturbation peut être caractérisée par la probabilité de survenue de chaque intensité et par ses propriétés spatiales. Ainsi, l'ensemble des perturbations passées et futures de même nature peuvent être intégrées sous la forme d'un régime de perturbation. Un régime de perturbation se définit alors par une distribution spatio-temporelle en termes d'intensité ; les caractéristiques spatiales comprenant l'aire, la forme et le caractère discret ou diffus, et les caractéristiques temporelles comprenant la durée, la fréquence, l'intervalle de retour et éventuellement la période de rotation. Deux caractéristiques s'ajoutent à la notion de régime de perturbation (Sousa 1984) : la spécificité qui décrit la corrélation de la perturbation avec l'espèce, la classe de taille ou le stade de succession (par exemple, les sécheresses qui impacte plus sévèrement les arbres dominant) ainsi que la synergie qui décrit les affinités d'interactions avec les autres types de perturbations (i.e. interaction sécheresse – incendies). Bien que l'étude des perturbations ponctuelles joue un rôle essentiel pour la compréhension des mécanismes physiologiques par exemple, la compréhension de la pleine implication des perturbations au sens évolutif et écologique nécessite de passer à l'échelle du régime de perturbation (White & Jentsch, 2001). Harper (1977) introduit ainsi une distinction entre les « désastres », définis comme les événements qui se produisent assez fréquemment pour être des agents sélectifs de l'évolution et les « catastrophes », les événements si peu fréquents qu'ils ne jouent aucun rôle dans la sélection. La relation qui relie la fréquence et

l'intensité d'une perturbation est une problématique en soi et, on observe généralement des perturbations importantes et peu fréquentes associées à de petites perturbations fréquentes (Turner et al., 1998).

1.3. Intégrer la relation entre intensité et impact : régime d'impact

Une problématique fondamentale consiste alors à évaluer la relation entre l'intensité et l'impact des perturbations (Romme et al., 1998). Le terme d'impact est utilisé ici dans le cadre de l'écologie des perturbations, pour désigner les réponses écologiques et fonctionnelles produites par une perturbation, à chaque niveau d'organisation de l'écosystème. Plusieurs types d'impacts des perturbations ont été identifiés à savoir des réponses continues ou dépendantes d'un seuil (White & Jentsch, 2001). Mécaniquement, le type d'impact et les valeurs de seuils, lorsqu'elles sont pertinentes, dépendent à la fois du système et du processus étudiés. Par exemple, chez les arbres, on peut distinguer d'une part la mortalité, dont la probabilité s'étudie au travers des seuils qualitatifs empiriques ou physiologiques (Anderegg et al., 2015 ; Clifford, 2013), et d'autre part la réduction de croissance, corrélée de façon continue aux variables climatiques notamment via la dendroécologie (à l'exception faite des crises des croissances pouvant succéder à une forte sécheresse par exemple [Lebourgeois et al., 2005]). Une description complète de la relation entre intensité et impact nécessite la prise en compte de la vulnérabilité du système étudié ; des peuplements forestiers, des espèces ou des individus de la même espèce pouvant répondre de façons très différentes à une même intensité (Cailleret et al., 2014). Si les traits fonctionnels qui modulent la sensibilité dépendent de la nature de la perturbation considérée, il est tout de même possible d'en tirer des généralités. Ainsi, la sensibilité d'un arbre face à une perturbation peut se décomposer en facteurs de sensibilité à l'échelle de l'individu et de son environnement qui sont liés à : (1) l'environnement de l'arbre (sol, compétition, étagement de la végétation, etc.), (2) des cofacteurs individuels liés à l'âge, à la morphologie ou encore à la taille relative, c'est à dire le statut social, et absolue de l'arbre, ainsi qu'à (3) ses performances génétiques individuelles dépendantes, donc, de la diversité génétique de l'espèce ou de la population considérée (Seidl et al., 2011 ; Mérian & Lebourgeois, 2011 ; Santos-Del-Blanco et al., 2013 ; Heer et al., 2018). Par exemple, la probabilité de chute d'un pin liée à une tempête dépendra des facteurs de sensibilités liés à

sa hauteur, à l'homogénéité et à la densité de son peuplement (risque d'effet domino), à la profondeur du sol que ses racines peuvent prospector ainsi qu'à l'architecture de ses racines, sa capacité d'ancrage et les propriétés mécaniques de son tronc, trois traits sous contrôle génétique (Nicoll & al., 1995 ; Silen et al., 1993 ; Stokes et al., 1997).

L'intégration de la relation intensité - impact permet de traduire un régime de perturbation en un régime d'impact défini par une distribution spatiale et temporelle mesurée, cette fois-ci, en termes d'impact de l'aléa. Dans le cadre de ma thèse, je m'intéresse plus particulièrement aux impacts démographiques sur la croissance, la reproduction et la survie. Étant commun à chaque perturbation, toute perturbation peut être conceptualisée de la même façon : un événement stochastique impactant la survie, la croissance et/ou la reproduction des individus.

2. Altération des régimes de perturbations : la vulnérabilité des écosystèmes forestiers

2.1. Changement global : altération des régimes de perturbation en cours

Les régimes de perturbation ont été profondément altérés dans de nombreux écosystèmes forestiers au cours des dernières décennies, le changement climatique étant le moteur principal de ces changements (Dale et al., 2001 ; Seidl et al., 2011). Ainsi, une augmentation de la fréquence et de l'intensité des perturbations a été largement documentée, par exemple pour les incendies (Hanewinkel et al., 2011), les tempêtes (Kamimura et al., 2017), les épidémies d'insectes (Paritsis & Veblen, 2011) et les sécheresses (Allen et al., 2015). Par exemple, la fin des années 1980 est marquée, en Europe, par une augmentation nette de l'intensité et de la fréquence des sécheresses climatiques estivales liée aux changements de régime des précipitations (ONERC). Associées à l'augmentation des températures moyennes, l'évaporation des sols et l'évapotranspiration par la végétation s'en trouvent exacerbées et on observe une banalisation des événements extrêmes de déficit hydrique des sols superficiels associée à une aggravation progressive qui pourrait atteindre, à la fin du XXI^e siècle, un niveau d'humidité moyen équivalent aux événements extrêmement secs de la période de référence 1961-1990 (Rapport final du projet ClimSec : Soubeyroux et al., 2011).

De plus, des changements dans les interactions entre perturbations ont été identifiés pour de nombreux facteurs de perturbations abiotiques (incendie, sécheresse, vent, neige et gel) et biotiques (insectes et pathogènes). Dans ce contexte, il convient de noter que la grande majorité des effets d'interaction entre perturbations rapportés dans la littérature sont synergiques, c'est-à-dire qu'ils amplifient l'intensité, l'occurrence et / ou l'impact des perturbations. Par exemple, en Europe, la dérive vers des conditions plus sèches et plus chaudes augmente particulièrement la probabilité d'occurrence des sécheresses. Parallèlement, le métabolisme des scolytes, notamment leur reproduction (Jönsson et al., 2011), est stimulé par la température. À la suite d'une sécheresse ou de sécheresses répétées, les scolytes peuvent se reproduire massivement sur les arbres déshydratés, ou affaiblis (chute

des réserves carbonées), conduisant à une explosion de leur population et des dépérissements, comme observé chez l'épicéa (*Picea abies*) en plaine en France.

2.2. Notion de risque d'effondrement

De telles altérations des régimes de perturbation peuvent avoir un impact important sur la capacité des forêts à fournir des services écosystémiques à la société (Thom & Seidl, 2016). De plus, celles-ci induisent le risque de dépasser la résilience écologique des forêts, et d'entraîner une modification durable des écosystèmes voire des déplacements vers des écosystèmes non forestiers à mesure que des points de basculement sont franchis (Reyer et al., 2015 ; Johnstone et al., 2016 ; Seidl et al., 2016). De nombreux exemples récents de mortalité à grande échelle due aux sécheresses et aux canicules dans le monde suggèrent qu'aucun type de forêt ou de zone climatique n'est invulnérable face aux changements de régimes de perturbations, même dans des environnements qui ne sont habituellement pas considérés comme limités en eau (Allen et al., 2010).

La vulnérabilité à de telles altérations est complexe et multifactorielle. Localement, elle dépend en particulier de facteurs de sensibilité prédisposant à atteindre un certain niveau de dommages comme déjà évoqués et de la capacité des populations impactées à s'adapter aux changements environnementaux (Kramer et al., 2010 ; Allen et al., 2015). La capacité d'adaptation intrinsèque des populations est un sujet controversé. Ainsi, certains auteurs s'inquiètent de la limite du potentiel d'adaptation du fait que : (1) le changement climatique est rapide par rapport au temps séparant deux générations d'arbres (Davis & Shaw, 2001), (2) les populations pourraient dans certains cas ne pas avoir le potentiel génétique adéquat pour s'adapter aux conditions environnementales changeantes (Davis & Kabinski, 1992) et (3), lorsque c'est nécessaire, les populations pourraient ne pas avoir la capacité de migrer suffisamment rapidement vers de nouveaux habitats disponibles, fait aggravé par la fragmentation des paysages (Jump & Penuelas, 2005). Cependant, d'autres auteurs mettent en avant le potentiel des mécanismes qui limitent la vulnérabilité des peuplements aux changements environnementaux (Hamrick & Godt, 1996). Ainsi, (1) les arbres montrent une plasticité phénotypique élevée qui leur permet de résister à de grandes fluctuations environnementales au cours de leur vie (Rehfeldt et al., 2002), (2) dans de nombreux cas, la variabilité génétique réside majoritairement au sein de chaque population plutôt qu'entre

populations (Leonardi & Menozzi, 1995 ; Buiteveld et al., 2007), et (3) des flux génétiques (en particulier dus au pollen) peuvent se produire sur de grandes distances entre des peuplements isolés, échangeant ainsi des ressources génétiques dont le bilan sera probablement favorable (Petit & Hampe, 2006 ; Kremer et al., 2012). Ce risque d'effondrement des populations a donc une dimension démographique, lorsque la mortalité excède la régénération, mais également, à plus long terme, une dimension génétique pour le maintien du potentiel adaptatif (Chevin et al., 2010) ; ces deux dimensions interagissent l'une avec l'autre.

2.3. L'enjeu de la biodiversité : cas de la diversité génétique

La diversité génétique est un facteur de la biodiversité indispensable à l'adaptation des espèces et des populations. La diversité génétique a été notamment corrélée à une meilleure résilience des écosystèmes après une perturbation (Procaccini et al., 2007), par exemple en réduisant l'impact dû aux ravageurs et aux maladies (Burton et al., 1992 ; Prospero & Cleary, 2017). Son implication dans le maintien des populations se manifeste pleinement lorsqu'il devient nécessaire de répondre à une maladaptation, c'est-à-dire lorsque l'optimum phénotypique s'éloigne de la valeur phénotypique de la population. Lorsque l'évolution contemporaine est possible (Wake, 2017), elle doit être assez rapide pour favoriser la persistance de la population dans des intervalles de temps extrêmement courts à l'échelle de l'évolution, et, avant tout, à la condition, entre autres, que le potentiel génétique autorise une telle adaptation. Une adaptation qui se produit suffisamment rapidement pour empêcher l'extinction due à un décalage adaptatif face à de nouvelles conditions environnementales est appelée sauvetage évolutif (Gomulkiewicz & Holt, 1995 ; Gonzalez et al., 2013). Les caractéristiques du sauvetage évolutif sont une série chronologique démographique en forme de 'U' formée d'une phase de déclin, puis de stabilisation et enfin de récupération en lien avec l'augmentation de la fréquence des génotypes adaptés aux nouvelles conditions environnementales au sein de la population (Carlson et al., 2014). Un point essentiel du sauvetage évolutif est que la sélection des génotypes adaptés est responsable du rebond démographique observé.

En particulier pour les organismes à longue durée de vie, on considérerait habituellement que les changements dans la composition génétique d'une population se

produisaient trop lentement pour que la variation génétique n'alimente un changement adaptatif appréciable sur quelques générations (Bell, 2013). Toutefois, un nombre croissant d'études suggèrent que, lorsque la sélection est forte, des réponses physiologiques, démographiques et évolutives peuvent toutes se produire à l'échelle écologique, sur quelques générations seulement (Pelletier et al., 2007, 2009 ; Hendry 2017 ; Govaert et al. 2019). L'héritabilité des traits adaptatifs, et, plus globalement, l'ensemble des paramètres génétiques de la population (variance et corrélations génétiques, déséquilibres de liaisons, etc.) déterminent le potentiel et la vitesse d'évolution, et donc notamment la probabilité de sauvetage évolutif. En outre, l'immigration et les flux de gènes devraient avoir un effet net positif par l'afflux d'une nouvelle diversité génétique assimilable à une nouvelle source d'options pour l'adaptation (Lenormand, 2002). En effet, si les flux de gènes peuvent avoir des effets à la fois positifs (par l'apport de diversité) et négatifs (en introduction une maladaptation), chez les arbres on s'attend à ce que le bilan soit globalement positif dans le contexte du changement climatique (Kremer et al., 2012).

2.4. Vers un risque d'effondrement grandissant

Le changement climatique, à travers l'altération des régimes de perturbations, aura des conséquences sur la diversité génétique intraspécifique à bien des égards. Celles-ci incluent notamment (1) des changements dans la distribution de la diversité génétique dans l'espace et dans le temps à mesure que l'aire de répartition des populations et des espèces changent, (2) des changements du niveau de plasticité phénotypique des individus et des populations répondant à de nouveaux stress environnementaux ainsi que (3) l'adaptation aux conditions environnementales changeantes (Hoffmann & Sgrò, 2011) pouvant notamment, mais pas exclusivement, accompagner un sauvetage évolutif. Dans de nombreux cas, ces changements impliquent une réduction de la diversité génétique des populations et des espèces à l'échelle locale comme globale (voir Pauls et al., 2012 pour le développement complet de ces processus), l'appauvrissement génétique contribuant à la réduction de la viabilité et au risque d'extinction de populations.

Dans le cadre de ma thèse, je me focalise exclusivement sur la microévolution aux échelles de temps écologiques. Les implications des perturbations sur la dynamique et la diversité génétique des forêts sont ainsi étudiées à court et moyen terme, sur quelques

génération. Si les processus micro-évolutif adaptatif n'induisent que peu de perte de diversité allélique aux échelles de temps étudiées (Le Corre & Kremer, 2003), en revanche, ils induisent des changements de variance phénotypique et génétique des traits adaptatifs par la sélection des combinaisons génotypiques favorables. Lorsque la sélection amène à une diminution de la variance génétique des traits sélectionnés, elle en fait de même pour les traits qui leur sont corrélés. Par conséquent, une émergence rapide de multiples événements de stress environnementaux (sécheresses, canicules, épidémies de ravageurs, etc.) pourrait dépouiller une population de son potentiel évolutif. Les perturbations peuvent également conduire à une réduction non spécifique de la taille efficace de la population en augmentant la mortalité et en réduisant le taux de fécondité (Lande 1993 ; Reed 2005). Si la population devient trop petite ou trop peu dense, elle sera soumise à (1) des processus démographiques tels que la limitation par le pollen lié à la diminution de probabilité de rencontre gamétique et (2) des processus génétiques tels que la dépression de consanguinité associée à un faible flux génétique, la fixation allélique due à la dérive génétique et, globalement, la perte de sa diversité. Combinés, ces processus démographiques et génétiques peuvent entraîner une diminution de valeur sélective de la population et ainsi augmenter son risque d'extinction (voir effet Allee). De telles conditions de stress démo-génétique peuvent alors initier un vortex d'extinction où la diminution de la diversité génétique elle-même entraîne une chute de la résilience aux stress (Soulé 1986 ; Fagan & Holmes 2006 ; Luque et al., 2016). Dans le contexte du changement climatique, on s'attend globalement à une augmentation du stress démo-génétique.

3. Le cadre de l'approche risque et multirisque

Le terme de risque recoupe une large gamme de définitions possibles, qui dépendent essentiellement de l'objet sur lequel porte l'analyse. Il n'y a pas, à l'heure actuelle, de consensus sur la manière de mesurer et de combiner les composantes intrinsèques du risque, mais quel que soit le modèle adopté pour l'évaluation, le résultat devrait être le même (Foerster, 2009) : le risque doit exprimer la probabilité de conséquences nuisibles ou de pertes attendues (perturbation de la production, dommages à l'environnement, perte de diversité, etc.) résultant de l'interaction entre la survenue d'aléas et des conditions de vulnérabilités (UNISDR, 2004).

3.1. Le risque, un concept multi-facette

Dans le cadre de l'étude du risque face aux aléas naturels et au changement climatique, la notion de risque peut être déclinée en trois composantes principales (Kron, 2005) : (1) **l'aléa** en lui-même se définit comme la probabilité qu'une perturbation menace ou affecte une zone donnée et se caractérise par sa magnitude et sa probabilité d'occurrence. (2) **L'enjeu** du risque représente la valeur globale des éléments exposés et menacés dans un système territorial donné. Ces éléments se rapportent à divers types de biens, écosystèmes, être vivant et niveaux de diversités, notamment génétique, pouvant être affectés. (3) **La vulnérabilité** quantifie la prédisposition d'atteindre ou d'excéder un état de dommages (ou de perte) donné suivant la nature et l'intensité de la perturbation.

A l'échelle de quelques générations, la vulnérabilité d'une population dépend de sa capacité d'adaptation. Ainsi, dans le cadre de ma thèse, la capacité d'adaptation sera considérée comme une composante à part entière de la vulnérabilité d'une population. Ainsi, la vulnérabilité peut se décomposer en deux termes (Petit, 2020) : la sensibilité et le potentiel adaptatif. D'une part, la sensibilité module les dommages spécifiques engendrés par l'aléa au travers de la combinaison des propriétés (faiblesses ou forces) intrinsèques de l'écosystème et des organismes qui le composent en fonction, notamment, de leur plasticité et de leur acclimatation à l'échelle de leur durée de vie. D'autre part, la capacité d'adaptation représente le potentiel évolutif des populations, c'est-à-dire leur capacité à modifier leurs traits fonctionnels au fil des générations afin de mieux faire face aux agressions (extrêmes

climatiques, par exemple). On peut résumer par : **Risque = Aléa × vulnérabilité (= sensibilité + capacité d'adaptation) × enjeu** (Fig. 1).

Si l'on reprend l'exemple du risque tempête, le risque "immédiat" de chute d'un pin dans une plantation dépend des facteurs modulant la sensibilité que sont la hauteur individuelle de l'arbre, l'homogénéité et la densité du peuplement (effet domino), la profondeur du sol qui peut être prospectée par les racines, ainsi que des traits adaptatifs sous contrôle génétique (allocation vers les racines pour l'enracinement par exemple). La composante suivante, l'enjeu, résulte de l'interaction entre la valeur intrinsèque du peuplement et son exposition à l'aléa (la direction des vents et reliefs par exemple). A une échelle de temps plus longue, le risque d'effondrement démographique lié à cet aléa dépendra des impacts résultant de l'interaction entre l'aléa, l'exposition et la sensibilité, mais également du potentiel du peuplement à se régénérer (sa résilience) et à s'adapter, dépendant de traits d'histoire de vie de l'espèce tels le temps de génération ainsi que de caractéristiques génétiques tels que la diversité génétique et l'héritabilité de traits adaptatifs (Fig. 1). Cet exemple illustre bien le fait que les impacts des aléas naturels varient avec l'échelle temporelle considérée.

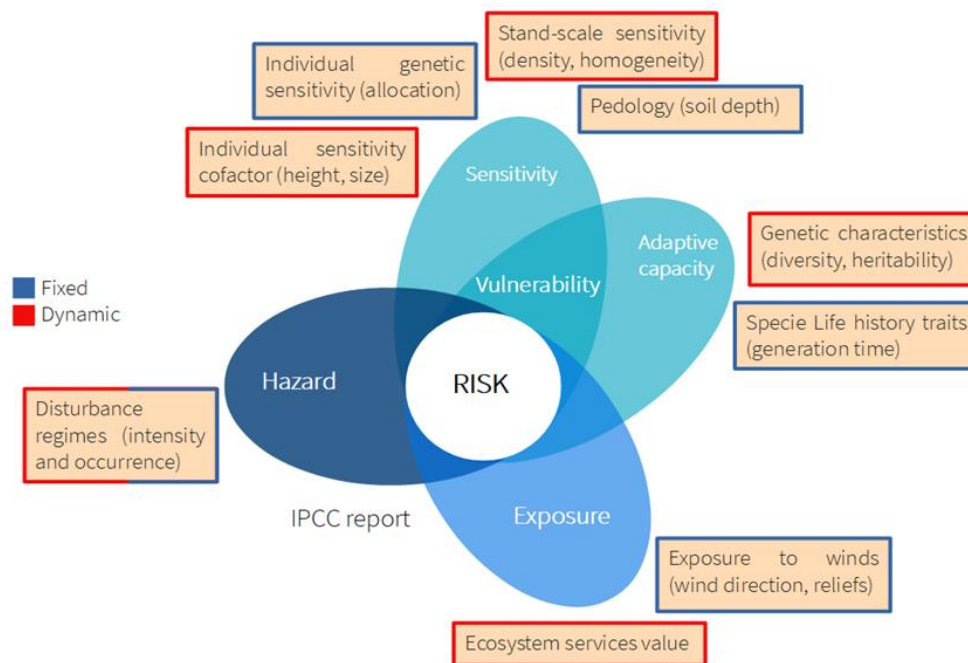


Figure 1. Identification des facteurs déterminants les différentes composantes du risque. Schéma conceptuel du risque sous la forme d'une « fleur » (Adapté d'après le GIEC/IPCC et Petit, 2020) : la notion de risque émerge lors de la rencontre entre un enjeu, un aléa et la vulnérabilité du système à cet aléa. A l'échelle de la microévolution, le risque d'effondrement d'une population dépend de sa capacité d'adaptation. Chaque composante du risque est déterminée par de multiples facteurs (facteurs de vulnérabilité et d'exposition) spécifiques à l'aléa considéré ; ici est présenté l'exemple de l'aléa tempête. Selon l'échelle de temps, certains facteurs peuvent être considérés comme étant fixes (la profondeur du sol par exemple) ou dynamique (la structure du peuplement).

3.2. Introduction à la gestion des risques en forêt

La gestion du risque se rapporte alors aux méthodes qui consiste à prendre des décisions face à l'incertitude des phénomènes biotiques et abiotiques extrêmes à venir (Seidl et al., 2017). Le processus de gestion des risques comprend trois étapes principales (Hanewinkel et al., 2011) : (1) l'évaluation du risque, y compris l'identification du type d'aléa, l'estimation de sa probabilité ainsi que des interactions possibles avec d'autres risques et la gravité des impacts associés, (2) l'identification des stratégies de gestion envisageables et leurs conséquences, et (3) la mise en œuvre du plan de gestion, c'est-à-dire la maîtrise du risque par l'application des stratégies envisagées. Deux particularités pour leur application aux écosystèmes et notamment aux milieux forestiers sont à noter. Premièrement, les propriétaires forestiers ou les gestionnaires peuvent ne pas partager la même aversion pour

le risque (Hummel et al., 2009). Cela signifie que, dans les écosystèmes forestiers, les opinions diffèrent sur la façon d'utiliser les résultats de l'évaluation des risques pour les décisions de gestion (Hanewinkel et al., 2011). Deuxièmement, la gestion du risque en forêt suppose une évaluation relative qui dépend des services écosystémiques rendus, de leur vulnérabilité aux aléas ainsi que de nos objectifs et besoins en termes de hiérarchisation et d'état fonctionnel de ces services. La nature multifonctionnelle des forêts impose de penser la gestion des services écosystémiques et la gestion des risques de façon globale, chaque choix de gestion pouvant influencer, et potentiellement de façon antagoniste, plusieurs services et risques. L'évaluation du risque en forêt nécessite donc la mise en place d'une approche multidisciplinaire et multirisque afin de tenir compte non seulement des impacts physiques (production) mais également de facteurs moins quantifiables tels que les facteurs environnementaux ou sociaux (Eriksson et al., 2018 ; Eriksson, 2017).

4. Gestion et pratiques sylvicoles : mieux intégrer la gestion des risques

Nous avons défini le risque comme l'interaction entre un aléa, la vulnérabilité (sensibilité et capacité d'adaptation) et l'exposition. Tout changement de l'un de ces composantes entraînera un changement correspondant du niveau de risque. La gestion forestière peut agir sur les trois composantes du risque. Les pratiques sylvicoles sont généralement conçues pour optimiser un ou plusieurs services écologiques (production de bois, protection des sols, conservation de la biodiversité, etc.), influençant par conséquent l'enjeu des forêts. Changer les objectifs assignés à la forêt est déjà une première approche de la gestion du risque, témoignant de la relation entre gestion du risque et services écosystémiques. Par exemple, changer l'objectif de production de bois d'œuvre pour une gestion tournée vers un objectif de protection des sols ou de récréation peut changer complètement l'évaluation du risque et sa gestion. Toutefois, si les gestionnaires peuvent être réticents à l'idée de contraindre ces services et donc la valeur des forêts (Jactel et al., 2009), il est en revanche aujourd'hui indispensable de trouver les compromis dans les décisions de gestion qui permettront de minimiser à la fois la probabilité d'occurrence des perturbations et la sensibilité des peuplements à celles-ci, tout en valorisant la capacité d'adaptation et la résilience des forêts dans un objectif de viabilité durable des services écosystémiques rendus (Millar et al., 2007).

4.1. La gestion pour agir sur l'aléa et la sensibilité

Le choix des essences plantées ou favorisées, les opérations d'éclaircie (intensité et fréquence) et de récolte ainsi que le type de régénération auront tous des effets importants sur la structure, la composition et la dynamique des peuplements forestiers et, par conséquent, sur la présence de facteurs de perturbation et sur la sensibilité des peuplements aux ravageurs (Wainhouse 2005), aux agents pathogènes (Tainter & Baker 1996), au vent (Quine et al., 1995), aux incendies (Peterson et al., 2005) ou encore aux sécheresses (Metz et al., 2016). Jactel et al., (2009) donnent un cadre d'analyse exhaustif sur les connaissances des effets de la gestion forestière à la fois sur l'aléa et sur la sensibilité à différents facteurs de perturbation. Il en ressort que la plupart des interventions sylvicoles affectent

considérablement à la fois l'occurrence et l'intensité de nombreux aléas biotiques et abiotiques ainsi que la sensibilité des forêts aux facteurs de stress qui menacent la productivité et la durabilité des écosystèmes forestiers.

En particulier, l'éclaircie, l'un des traitements sylvicoles les plus couramment appliqués dans le monde notamment pour atteindre des objectifs de production, pourrait aussi être un outil efficace pour améliorer la résistance et la résilience des forêts à de multiples facteurs de stress associés au changement global (Moreau et al., 2022). L'éclaircie réduit les impacts négatifs de la sécheresse, car la réduction de la densité du peuplement peut augmenter la disponibilité en eau pour les arbres restants (Sohn et al., 2016 ; Schmitt et al., 2020 ; Gavinet et al., 2020). Les éclaircies précoces ont le potentiel de réduire la vulnérabilité aux dommages causés par le vent notamment en favorisant le développement des racines structurales. Cependant, dans un peuplement mature, l'éclaircie peut augmenter la vulnérabilité aux dommages causés par le vent en réduisant la stabilité du peuplement et en augmentant la charge de vent sur les arbres restants. L'éclaircie réduit le risque et la gravité des incendies en réduisant la charge en combustible et en perturbant la continuité du combustible dans le peuplement. L'effet positif observé sur les incendies augmente lorsque l'éclaircie concerne les arbres dominés, c'est-à-dire une éclaircie par le bas. L'éclaircie peut atténuer l'impact des infestations d'insectes et d'agents pathogènes en réduisant la densité des hôtes et en réduisant la connectivité entre les arbres hôtes lorsqu'ils sont, par exemple, dispersés parmi d'autres espèces.

Cependant, différentes opérations sylvicoles, et même différentes options pour chaque opération, auront des effets multiples et parfois contradictoires sur la sensibilité des peuplements à divers types de facteurs de perturbation (Jactel et al., 2009 ; Moreau et al., 2022). Par exemple, lorsqu'une éclaircie réduit la compétition pour les ressources (eau, nutriments, etc) et améliore ainsi la vigueur des arbres, elle peut réduire leur sensibilité à un certain nombre de ravageurs secondaires, notamment les scolytes. Pourtant, l'accroissement de la lumière sous couvert succédant à l'éclaircie peut aussi favoriser les insectes ravageurs, notamment les scolytes, et des températures plus élevées sous couvert favorisent un plus grand nombre de générations d'insectes pendant la période de végétation (Taylor et al., 1996 ; Fettig et al., 2007). Afin d'amoindrir le risque global dû aux perturbations actuelles et futures, il est donc nécessaire de considérer l'ensemble des aléas présents et leurs interactions,

notamment indirectes au travers de la gestion. Ainsi, c'est la prévalence régionale des risques qui doit permettre d'évaluer quels aléas ou complexes d'aléas traiter en priorité et qui détermine la meilleure stratégie de gestion en fonction des enjeux locaux.

4.2. Le choix de la ressource génétique pour contrôler la sensibilité

Une fois qu'une essence a été choisie pour le boisement, en particulier en peuplements purs, la sélection de matériel génétique pour un site spécifique est une étape clé de la planification forestière alors que les matériels forestiers de reproduction (MFR)¹ possèdent des caractéristiques génétiques contrastées. Entre autres implications, ce processus de sélection peut prévenir ou limiter les dommages liés aux perturbations actuelles ou anticipées en rejetant les ressources génétiques sensibles dans les zones à risque pour un facteur de perturbation donné (Wingfield & Swart, 1994). Ainsi, la sélection et la plantation de génotypes tolérants, résistants et/ou résilients pourrait être une stratégie efficace pour minimiser les pertes actuelles et anticipées par des facteurs de perturbations biotiques et abiotiques (Jactel et al., 2009). Le challenge principal de cette approche consiste à faire ce choix dans le cadre du changement climatique et de ses incertitudes. Évaluer les risques existants et identifier leur évolution et les risques émergents ne suffit pas : il s'agit de considérer le fait qu'une ressource génétique qui sera bien adaptée dans 50 ans ne l'est pas nécessairement aujourd'hui et inversement (Lefèvre, 2012). De plus, cette stratégie, qui implique un contrôle total du matériel génétique utilisé, soulève plusieurs problèmes. Localement, c'est l'ensemble des aléas, leurs interactions ainsi que la covariation des facteurs de sensibilité à ces aléas au travers du paysage génétiques et des opérations sylvicoles qui déterminent les optimums génotypiques pour la meilleure valeur adaptative. Ces contraintes multifactorielles rendent difficile, si ce n'est impossible, l'accès à ces optimums par la plantation de génotypes sélectionnés. Plus encore, ces optimums théoriques se déplacent au cours du temps à mesure que les régimes de perturbation sont altérés, que les ravageurs évoluent et s'adaptent (Neuhauser et al., 2003) et que les pratiques sylvicoles tendent aussi à s'adapter à ces changements. Une grande maîtrise de la magnitude environnementale actuelle et future du site de plantation et de la gamme de variations endurable par la

¹ Les matériels forestiers de reproduction (MFR) sont constitués de ressources génétiques forestières (RGF) d'une grande variabilité en termes d'adaptation aux conditions pédo-climatiques actuelles et futures.

ressource génétique utilisée sont donc indispensables. Le dépérissement massif du pin maritime dans les Landes de Gascogne à la suite des introductions de graines d'origine ibérique et des grands froids des années 1962-1963 et 1985 est un exemple saisissant d'une évaluation du risque incomplète (de la sensibilité et de l'aléa) liée à la sélection de la ressource génétique (Le Tacon et al., 1994). En effet, les génotypes d'origine ibérique ont été valorisés pour la plantation de par leur résistance à la cochenille *Matsucoccus feytaudi*, alors que leur sensibilité au froid n'a été identifiée que trop tardivement, ces conditions climatiques de grand froid n'étant rencontrées que rarement dans cette région. En outre, cette stratégie concerne les forêts régénérées artificiellement, alors que plus de 80 % de la forêt française est issue de régénération naturelle.

4.3. La capacité d'adaptation vue comme un facteur de moindre vulnérabilité

Au sein d'un peuplement, les choix des opérations d'éclaircie (intensité, fréquence, systématique, sélective), de récolte (choix des arbres semenciers), d'élagage ou les traitements chimiques (épandage pour limiter la végétation concurrente ou les ravageurs) et mécaniques (labour, ripage) auront également des effets sur les contraintes environnementales, le système de reproduction ainsi que l'intensité de la sélection phénotypique par le forestier, et par conséquent, sur l'ensemble des paramètres génétiques du peuplement. Que ce soit volontaire ou non, toute pratique sylvicole a donc des conséquences sur les processus évolutifs. Lefèvre et al., (2014) donnent un cadre d'analyse exhaustif sur les connaissances des effets des options de gestion sur les processus évolutifs.

Lefèvre et al. (2014) identifient cinq mécanismes majeurs d'influences des opérations sylvicoles sur la vulnérabilité des peuplements au travers de leur capacité d'adaptation : (i) Une conséquence générale de la sylviculture sur les moteurs de l'évolution est le changement des conditions environnementales. Les facteurs environnementaux (dont la concurrence) déterminent l'expression de la variance phénotypique et génétique (lors d'interactions Génotype × Environnement) des caractères et le gradient de sélection qui relie la valeur des traits fonctionnels à la valeur sélective. La réduction systématique des facteurs de stress peut alors être un frein à l'évolution à cause d'une faible mortalité liée à la sélection naturelle dans les peuplements (Kuparinen et al., 2010). (ii) Le niveau de fermeture du couvert, modulé par

la fréquence et l'intensité des éclaircies, affecte les paramètres de dispersion du pollen et du système de reproduction : une faible densité d'arbres reproducteurs augmente simultanément la probabilité individuelle de se reproduire et la diversité des croisements qui peut s'expliquer mécaniquement par un taux plus élevé de pollinisation à longue distance (Klein et al. 2006). (iii) Une éclaircie, qu'elle soit systématique ou sélective, affecte l'agrégation spatiale des arbres reproducteurs génétiquement apparentés et, par conséquent, la structure du système de reproduction. Par exemple, la suppression des individus apparentés, lors d'une éclaircie, peut réduire la structure génétique spatiale et le coefficient de consanguinité de la régénération (Dounavi et al., 2002). (iv) Dans les populations de faible effectif, la réduction du nombre d'arbres reproducteurs affecte l'effectif efficace et peut conduire à une réduction de la diversité génétique par la perte d'allèles rares potentiellement bénéfiques ou délétères (Buchert et al. 1997 ; Rajora et al. 2000). L'intensité de la dérive génétique, au travers de la variance du succès de reproduction et du système de reproduction dépend donc non seulement du nombre et de la distribution spatiale des arbres reproducteurs mais aussi de leur contribution relative à la reproduction. (v) Dans les peuplements régénérés naturellement, la variance et la moyenne des valeurs génétiques des arbres reproducteurs résultent de l'intensité de sélection des éclaircies sélectives successives sur des critères de valeur phénotypique telles que leur taille, leur statut social, l'absence de défauts, l'état sanitaire, etc. Des caractères liés à la vigueur et à la sensibilité aux aléas peuvent être indirectement sélectionnés. Lorsque ces caractères covarient avec la valeur sélective, on s'attend à ce que les opérations sylvicoles accélèrent l'adaptation des populations. Or, les caractères de résistance peuvent également être négativement corrélés avec les caractères de croissance ou de qualité du bois (Kleinhentz et al., 1998). Ces corrélations peuvent résulter d'interactions fonctionnelles entre les traits impliqués dans la croissance et dans la modulation de la sensibilité à différents aléas ou de contraintes génétiques résultent de l'architecture génétique de ces traits (gènes épistatiques ou pléiotrope, déséquilibre de liaison, etc.). Dans ce cas, les opérations sylvicoles pourraient contraindre ou limiter le processus de sélection pour des caractères modulant la sensibilité des arbres aux aléas, et, globalement l'adaptation des peuplements à de nouvelles conditions environnementales.

Ainsi, dans l'objectif d'adapter les forêts au changement climatique, outre la première stratégie déjà évoquée qui implique un contrôle total du matériel génétique utilisé, une seconde stratégie consiste, quant à elle, à prendre en compte et à piloter les processus micro-évolutifs dans une pratique adaptative de la sylviculture pour renforcer la capacité des forêts à répondre spontanément aux changements climatiques (Lefèvre et al., 2014). L'objectif d'une telle stratégie consiste donc à identifier, à entretenir, voire accélérer les processus évolutifs naturels en favorisant la ressource génétique locale, déjà adaptée à son environnement actuel. Les trois objectifs principaux seraient : (1) augmenter les chances d'émergence de combinaisons génétiques « innovantes », (2) faciliter la sélection et la diffusion des géotypes les mieux adaptés et (3) préserver la diversité génétique pour une réponse à long terme à la sélection. Ceci est supporté par les processus démo-génétiques spontanés que sont la régénération naturelle et la sélection naturelle. Cette stratégie ne peut produire que des changements progressifs et limités par le potentiel évolutif de la ressource locale, mais elle oriente vers une adaptation aux conditions locales spécifiques et assouplit l'incertitude écologique liée à l'introduction de matériel génétique étranger seul.

L'enrichissement génétique de la ressource génétique locale par l'introduction d'une certaine quantité (à déterminer) de matériel allochtone d'une origine présumée pré-adaptée, pourrait permettre d'introduire des allèles d'intérêt. Associée à une gestion par l'évolution, cette option semble ne conserver que les avantages des deux stratégies précédentes, associant une meilleure maîtrise du risque à une amélioration du potentiel adaptatif, a priori, plus radicale.

III - Objectifs et démarche générale de l'étude

1. Objectifs de l'étude

Ma thèse vise à mieux comprendre les multiples effets d'interactions entre les pratiques de gestion et les perturbations sur la dynamique démo-génétique des peuplements forestiers. Je m'intéresse plus particulièrement aux perturbations climatiques (sécheresses, canicules, gelées, tempêtes) et à leurs impacts sur la croissance, la reproduction, la survie et la diversité génétique des peuplements monospécifiques de sapin Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et de cèdre de l'Atlas (*Cedrus atlantica* (Endl.) Manetti ex Carrière). Mon hypothèse de travail est que la synthèse des connaissances sur ces impacts et leur intégration dans un modèle de dynamique forestière permettront de mieux raisonner notre marge d'action sur la sensibilité, la résilience et la capacité évolutive des forêts. Les connaissances à intégrer sont de trois ordres : des connaissances empiriques et mécanistes sur la dynamique démographique des peuplements, des connaissances empiriques et écophysiological sur les impacts des aléas et sur les facteurs de sensibilité associés, ainsi que des connaissances sur la variation phénotypique de la réponse aux aléas et les bases génétiques de cette variation.

Les impacts de la gestion et des perturbations sur la dynamique et la diversité génétique des forêts seront systématiquement analysés à court et moyen terme, sur un horizon temporel global de quelques cycles de régénération, ce qui est cohérent avec l'horizon de planification pour les gestionnaires forestiers. L'échelle spatiale considérée est le peuplement forestier. Les options de gestion correspondante sont les actions sylvicoles, les éclaircies et le choix des arbres semenciers par exemple.

Ma thèse s'inscrit dans un double objectif : identifier les mécanismes et les potentiels points de basculement pouvant conduire soit à l'effondrement soit au maintien des processus démographiques et évolutifs des populations, et identifier notre niveau de maîtrise du risque par la gestion. J'aborde ainsi deux grands types de questions, fondamentales et appliquées :

[1] Quels sont les processus éco-évolutifs qui façonnent la dynamique forestière ? Dans quelle mesure la diversité génétique et la microévolution peuvent-elles atténuer la

vulnérabilité d'une population d'arbres aux changements de régimes de perturbations et éventuellement la sauver de l'extinction ?

[2] Comment des stratégies de sylviculture adaptative peuvent-elles atténuer la vulnérabilité des forêts au changement climatique sur une échelle de temps écologique (c'est-à-dire sur quelques générations) comparativement à des recommandations plus classiques ? Ainsi, quels sont les risques, les coûts et les avantages de ces stratégies d'adaptation de la sylviculture au changement climatique pour nos forêts ? Comment raisonner des compromis entre les risques, les coûts et les avantages à court terme et sur quelques générations ?

Le développement d'une nouvelle approche par modélisation pose également des questions proprement méthodologiques [3] :

[3] Comment conceptualiser et modéliser concrètement des régimes d'impact dans une démarche évolutive individu-centrée ? Quels indicateurs du potentiel adaptatif sont pertinents dans l'évaluation des processus démo-génétiques ? Quels sont les paramètres du modèle les plus sensibles / les plus importants ?

La question de la validation du modèle sera aussi une question centrale dans le cadre de ma thèse.

2. Description générale de la démarche

La démarche proposée dans ma thèse consiste globalement en une interrogation sur le type d'outil pour mener à bien mon travail et leurs limites (article 1), le choix de tirer parti du modèle démo-génétique Luberon2 avec une première utilisation sur un cas d'étude, le cèdre, qui correspond à un exercice de validation qualitative de la démarche et d'identification de besoins d'amélioration, notamment pour prendre en compte les stress dans les interactions génotype x environnement x pratiques sylvicoles (article 2), l'utilisation d'outils complémentaires, comme le modèle écophysologique Castanea, pour mieux identifier les interactions entre le stress, la sensibilité et la vigueur des arbres (article 3), et l'intégration de ces résultats dans le modèle Luberon2 en prenant cette fois-ci le sapin Douglas comme cas d'étude.

Mon travail tire donc profit du modèle Luberon2, préexistant sur la plateforme Capsis², et qui possédait déjà une structure de couplage démo-génétique fonctionnelle pour le cèdre. Dans le cadre de ma thèse, j'ai adapté Luberon2 à une nouvelle espèce, le sapin Douglas, une espèce introduite en France en 1842 et utilisée en plantation dans un objectif principalement de production. Le sapin Douglas était une espèce cible du projet B4EST³ dans lequel s'inscrit ma thèse. En outre, le choix de cette espèce à été fait en fonction de la compatibilité avec Luberon2 d'un modèle de dynamique forestière préexistant sur la plateforme Capsis, des données d'impact des aléas disponibles et de l'intérêt de l'essence pour raisonner la capacité d'adaptation sur plusieurs générations. En effet, les vieilles forêts de sapin Douglas montrent souvent des conditions favorables à la régénération naturelle en Europe, alors que la plupart des forestiers hésitent encore quant à cette opportunité et à la manière d'en tirer parti (Petit & Claessens, 2013).

La démarche proposée dans ma thèse intègre l'impact des perturbations et des pratiques sylvicoles sur les fonctions démographiques de Luberon2. L'enjeu était de coupler

² Capsis est une plateforme de simulation de modèles de croissance et de dynamique forestière. C'est un outil pour les scientifiques forestiers, les aménagistes forestiers et l'éducation. Il est développé au laboratoire AMAP depuis 1999.

³ B4EST est un projet H2020 financé par l'UE qui se concentre sur la sélection adaptative pour des forêts productives, durables et résilientes face au changement climatique (<https://b4est.eu/>).

ces différentes composantes et d'intégrer la variation des facteurs de sensibilité, dont individuels, dans le couplage. Dans ce sens, j'ai développé la notion de régime d'impact en proposant un formalisme pour (1) les régimes de perturbations, c'est-à-dire la façon de mesurer l'intensité de l'aléa et l'analyse de la fréquence d'occurrence des différentes intensités, (2) les fonctions d'impacts démographiques sur la croissance, la reproduction et la survie et (3) les effets de cofacteurs modulant la sensibilité aux aléas à l'échelle du peuplement et des individus. Par la suite, l'implémentation du formalisme de régime d'impact dans la structure démo-génétique de Luberon2 et la simulation d'itinéraires sylvicoles classiques et originaux m'a permis de tester l'effet de ces itinéraires sur les performances, i.e. sensibilité aux aléas, croissance, survie et reproduction, et la qualité génétique de différents peuplements en place, ainsi que d'estimer leur potentiel adaptatif à court et moyen-terme.

IV - Le choix d'une approche par modélisation Démo-Génétique

1. L'approche par modélisation Démo-Génétique : un choix adapté aux questions de l'étude

De par les questions considérées au travers de ma thèse, les contraintes pour le choix de l'architecture du modèle sont multiples. Les moteurs des changements environnementaux doivent pouvoir être de natures diverses, y compris des perturbations pour lesquelles on ne connaît pas précisément l'ensemble des mécanismes physiologiques de réponse mais seulement des références empiriques sur les impacts démographiques (croissance, survie et reproduction). Le modèle doit être approprié à une problématique liée à l'évolution génétique sur une échelle de temps multigénérationnelle. Trois conditions sont requises pour qu'un modèle atteigne cet objectif (Oddou-Muratorio et al., 2020) : (1) le modèle doit être individu centré ; (2) le modèle doit décrire explicitement l'architecture génétique de la variation des caractères et (3) les processus de reproduction sexuée (recombinaison, etc.) doivent être inclus dans la partie démographique du modèle. En outre, l'intégration des processus démographiques aux processus évolutifs est requise pour modéliser les effets de la sylviculture, la plupart des pratiques forestières consistant en un contrôle démographique à l'échelle du peuplement. Chaque opération sylvicole a des impacts multiples sur les processus écophysiologiques, démographiques et évolutifs qui lui succèdent et influence ainsi les opérations suivantes et leurs impacts ; une approche dynamique de ces interactions est donc nécessaire. Le choix a été fait de s'orienter vers les modèles démo-génétique individu-centré (DG-ABM), pour un compromis de complexité satisfaisant.

Les modèles démo-génétiques intègrent la variabilité interindividuelle à l'échelle des traits d'histoire de vie uniquement. De par leur structure (Fig. 2), les modèles démo-génétiques forment une boucle de rétroaction éco-évolutive où (1) la diversité génétique et son architecture déterminent la structure démographique et la dynamique des populations, (2) la structure démographique et la dynamique des populations entraînent la dérive génétique, la sélection et le flux génétique, qui (3) déterminent, à leur tour, la diversité génétique et son organisation, etc. Ils ne présupposent aucune fonction de valeur sélective a

priori, mais permettent son émergence au travers de la dynamique de la population, via les relations sous-jacentes entre génotype et phénotype, entre phénotype et démographie ainsi qu'entre démographie et valeur sélective. En effet, les modèles démo-génétiques s'affranchissent d'une relation fixe entre les traits et la valeur sélective, qui serait moins appropriée dans le contexte du changement climatique, mais qui est généralement imposée par les modèles de génétique des populations et de génétique quantitative classiques. La flexibilité de ces interactions rend donc les modèles démo-génétiques particulièrement adaptés à une approche dynamique de l'évolution contemporaine.

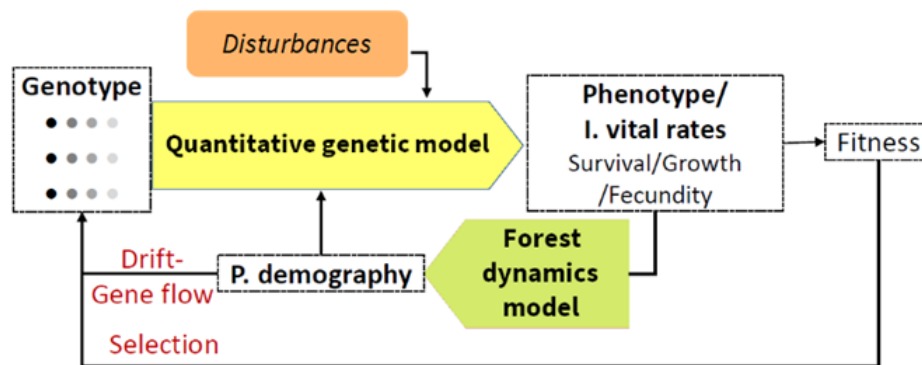


Figure 2. Adapté de Oddou-Muratorio et al., 2020. Cadre conceptuel pour le couplage des processus démographiques et évolutifs dans les modèles démo-génétiques. Les cases blanches représentent les variables d'état dynamique du système ; les cases colorées en forme de flèche représentent les différents modèles utilisés pour les simuler. Le texte rouge représente les processus évolutifs. I est l'abrégié d'individu, P de population. Dans la case Génotype, chaque ligne représente un locus, les différentes nuances de gris indiquant différents allèles.

2. Article 1 (publié). Importance of interindividual interactions in eco-evolutionary dynamics: the rise of demo-genetic agent-based models

Dans le cadre d'un réseau du département Ecologie et Biodiversité d'INRAE (ECODIV) sur les modèles démo-génétiques, nous avons rédigé un papier d'opinion centré sur ce genre de modèles : le bond conceptuel qu'ils représentent, leurs avantages et inconvénients, ainsi que les questions scientifiques et appliquées pour lesquelles ils semblent particulièrement adaptés. En particulier, nous exposons en quoi les DG-ABM sont pertinents pour (1) l'exploration de questions fondamentales en écologie évolutive telles que la compréhension des boucles de rétroaction éco-évolutives et l'évolution contemporaine et (2) l'aide à la décision pour évaluer les coûts et bénéfices évolutifs à court et à long terme des stratégies de gestion et pour évaluer les compromis potentiels. Nous listons des outils et des pratiques pour faciliter le développement des DG-ABM tel que la plateforme Capsis. Il s'agit d'un travail collectif et interdisciplinaire porté en particulier par les cinq doctorants du réseau, tous co-premiers auteurs, dont je fais partie (voir la section "*Author contribution*" de l'article pour plus de détail).

Cette section correspond à l'article en question, publié dans le journal *Evolutionary applications*⁴. Les annexes de cet article, comme ceux des autres articles de ce manuscrit de thèse, se trouvent en Annexe 1.

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Importance of interindividual interactions in eco-evolutionary population dynamics: the rise of demo-genetic agent-based models

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Abstract

The study of eco-evolutionary dynamics, which favours the convergence of ecological and evolutionary time scales, is of growing interest in the current context of global change. However, many eco-evolutionary studies overlook the role of interindividual interactions, which are hard to predict and yet central to selective values.

Here, we aim to put forward models that simulate interindividual interactions in an eco-evolutionary framework: the demo-genetic agent-based models (DG-ABMs). Being demo-genetic, DG-ABMs consider how ecological and evolutionary processes are intertwined. Being agent-based, DG-ABMs follow populations of interacting individuals with sets of traits that vary among the individuals. We argue that the ability of DG-ABMs to take into account the genetic heterogeneity - that affects individual decisions/traits related to local and

instantaneous conditions - differentiates them from analytical models, another type of model largely used by evolutionary biologists to investigate eco-evolutionary feedback (EEF) loops. Based on the review of studies employing DG-ABMs and explicitly or implicitly accounting for competitive, cooperative, or reproductive interactions, we illustrate that DG-ABMs are particularly relevant for the exploration of fundamental, yet pressing, questions in evolutionary ecology across various levels of organisation. By jointly modelling the effects of management practices and other eco-evolutionary processes on interindividual interactions and population dynamics, DG-ABMs are also effective prospective and decision support tools to evaluate the short- and long-term evolutionary costs and benefits of management strategies and to assess potential trade-offs. Finally, we provide a list of the recent practical advances of the ABM community that should facilitate the development of DG-ABMs.

Key-words: eco-evolutionary dynamics, demo-genetic models, eco-genetic models, agent-based models, DG-ABMs

Introduction

Understanding and anticipating populations' response to changes in environmental and anthropogenic pressures requires conceptual and modelling approaches coupling ecological and evolutionary processes. This is largely motivated by the increasing realisation that ecological and evolutionary responses of populations can occur on similar temporal scales, with potential consequences on dynamics from gene to ecosystem (Carroll *et al.* 2007). The burgeoning literature investigating eco-evolutionary dynamics illustrates this growing interest (Dunlop *et al.* 2009; Schoener 2011; Romero-Mujalli *et al.* 2019; Oddou-Muratorio *et al.* 2020; Bassar *et al.* 2021).

The conceptual framework of eco-evolutionary dynamics depicts feedback loops between response processes at different levels of biological organisation in a contemporary time scale (Pelletier *et al.* 2009; Hendry 2017; Govaert *et al.* 2019). These feedback loops acknowledge that (1) genetic diversity and its architecture determine the demographic structure and population dynamics through phenotypic expression; (2) demographic structure and population dynamics determine evolutionary processes, i.e., genetic drift, selection and gene flow, which in turn (3) determine genetic diversity. As an illustration of such feedback, the competition between trees within a forest results in a selection process contributing to genetic evolution, while the genetic composition of the tree population drives interindividual competition and forest productivity (Pretzsch 2021). To account for feedback loops, eco-evolutionary models must integrate inheritance mechanisms and the multiple driving forces controlling the dynamics of the distributions of heritable traits across generations (Bassar *et al.* 2021).

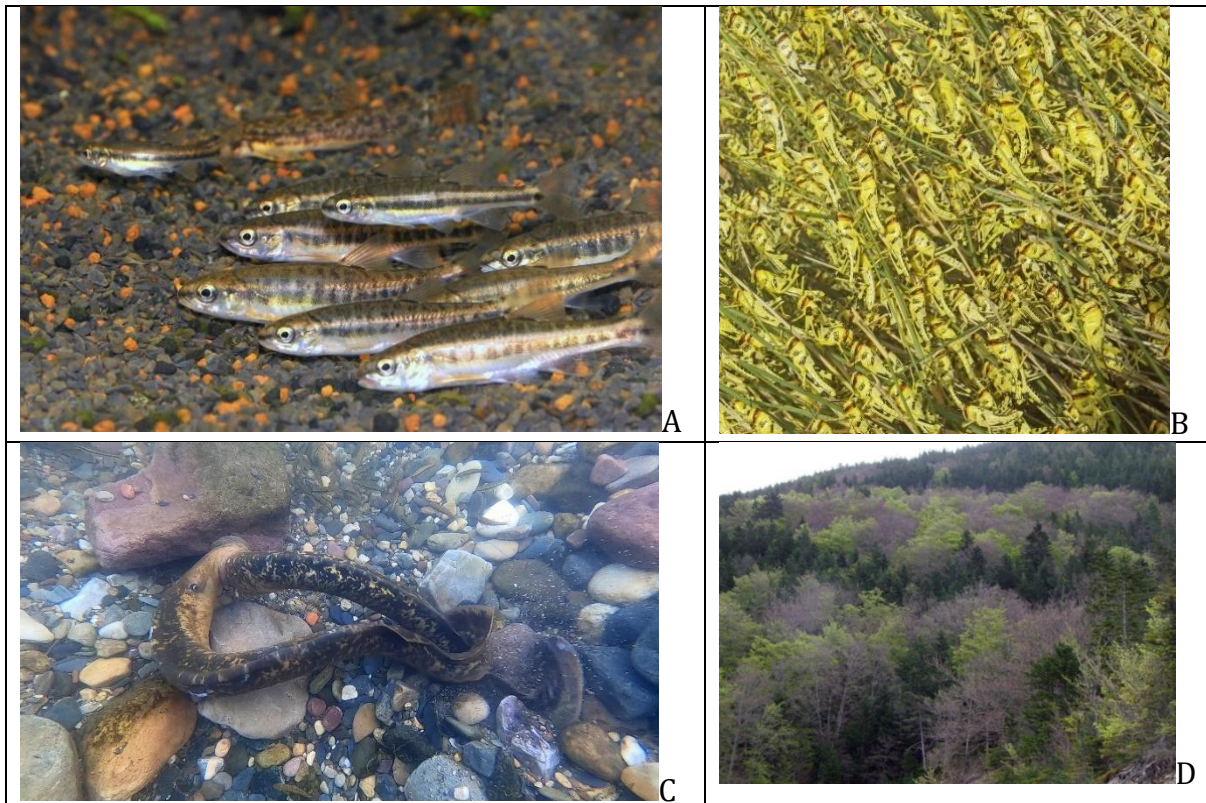
One of these key drivers of selection are the interactions between individuals within populations, as they directly or indirectly affect individual fitness at the core of any evolutionary dynamics (Maynard Smith 1974; Webber & Vander Wal 2018). We focus here on *within*-population interindividual interactions (i.e., competition, cooperation, and mating) affecting the demographic dynamics (growth, reproduction, mortality) and ultimately individual fitness or even inclusive fitness (Box 1). In essence, the outcome of such interactions is eminently stochastic and context-dependent, and population structure itself is part of the context. It is now recognised that the structure of social networks within a population may affect natural selection and traits evolution through indirect genetic effects (traits affected by genes in other individuals, Wade *et al.* 2010; Kazancioğlu *et al.* 2012; Fisher & McAdam 2017; Marjanovic *et al.* 2022). Additionally, these networks are themselves dynamic, since changing the social environment may influence an individual's later decisions in a social interaction, leading to rapid shifts in networks' structures (Farine & Whitehead 2015). For instance, individuals are able to modify their mating tactics, which diminishes the selection they endure (Oh & Badyaev 2010), and thus affects selection at the population level. Likewise, the distribution of phenological traits (e.g., flowering or maturation time) shapes mating opportunities within plant and animal populations, and possibly leads to assortative mating (here, the positive correlation of phenology between mates). Compared to random mating, assortative mating can either deplete or increase the genetic variance available for selection depending on whether the environment is stable or changing, with contrasted consequences on genetic adaptation (Godineau *et al.* 2021). Unfortunately, the interindividual interactions are usually little appreciated in eco-evolutionary models, with potential consequences on our understanding of the full range of eco-evolutionary responses.

Box 1: Interindividual interactions involved in population eco-evolutionary dynamics

Here, we focus on interactions between conspecific individuals within a population- mainly competition, cooperation, and mating - which directly drive the processes of mortality, growth, and reproduction (e.g., Figure A, C, D below) and whose variations subsequently induce evolutionary changes. This also includes the variety of ecological interactions indirectly impacting demography, such as exchange of information (e.g., on predator, or resource availability), movement (e.g., to escape predation or competition) or group behaviour (e.g., affecting predator's avoidance or resistance, Figure A, B below).

The major reason why we focus on local (i.e., within-population), variable, conspecific interactions is that evolution is a population-specific process, primarily fuelled by differences in individual fitness arising from the response to abiotic and biotic environments, the latter including the social context. Interspecific interactions may also shape the within-population social context and contribute to evolution: for instance, the existence and strength of plant-pollinator interactions define the social context within which selfing may evolve (Katsuhara *et al.* 2021). Trophic interactions may contribute to the resource context within which functional traits related to resource acquisition may evolve (Kang & Thibert-Plante 2017). On a macroevolutionary timescale, intra- and inter-specific competition for resources can drive speciation (Gavrilets *et al.* 2007; Weber *et al.* 2017). However, considering interspecific interactions without genetic variation in at least one of the partners of the interaction is not enough to model the dynamic feedback loop between ecological interactions, fitness, and the genetic composition of the population. This is

particularly why predation was not considered as a focal interaction in this review: indeed, when predation is investigated from the point of view of the variation of a prey's trait conferring variable avoidance ability from the predator, or from the variation of a predator's trait conferring variable ability to catch prey, then it becomes a trait involved in competition among prey to escape predators, or among predators to catch prey (e.g., Labonne & Hendry 2010b).



(A) School of common minnow (*Phoxinus phoxinus*) individuals maintained in an experimental tank at INRAE, Saint-Pée-sur-Nivelle, France. Schooling behaviour in this species is supposed to be both an anti-predator and a foraging optimisation strategy (Photo: ©INRAE - Stéphane Glise).

(B) Fifth instar hoppers of gregarious desert locust basking in the morning sun within herbaceous plants of the Mauritanian desert; grouping behaviours and bright coloration in desert locust (*Schistocerca gregaria*) are supposed to be an anti-predator strategy (Photo: © JIRCAS - Koutaro Ould Maeno).

(C) Sea lamprey (*Petromyzon marinus*) spawning in the Nive River (South-western France). Species from the Petromyzontidae family are semelparous, but the number of mates is highly variable among species (Photo: ©INRAE - Stéphane Glise)

(D) Beech (*Fagus sylvatica*) trees with late and early phenologies on Mont-Ventoux, France. Phenological mismatch limits male more than female reproductive success (Photo: ©INRAE – Frédéric Jean)

Our objectives here are to put forward models that explicitly *or* implicitly account for variable within-population interindividual interactions in an eco-evolutionary framework: the demo-genetic agent-based models (DG-ABMs). After defining these models, we survey the literature to illustrate how DG-ABMs can be used to investigate fundamental issues in evolutionary ecology, as well as to assist the management of natural populations facing environmental changes.

How to model eco-evolutionary feedback loops: from analytical models to DG-ABMs

At the very core of the eco-evolutionary models is the need of specifying the genetically variable and heritable traits, their impact on the focal organism's life history, and the ecological embedding that determines how life-history traits affect and are affected by environmental conditions and the demographic context (Dieckmann & Ferrière 2009). This can be achieved by various approaches (Figure 1). First, there is a long tradition in evolutionary ecology to rely on analytical models (differential-equation and difference equation models) which offer elegant solutions and provide general knowledge on elementary eco-evolutionary feedback (EEF) loops, generally at the cost of simplifying hypotheses. Among the most common analytical formalisms of EEF loops are (1) adaptive dynamics models (Dieckmann & Ferrière 2009), which incorporate ecological realism, in particular, the notion that the success of any given strategy depends on its frequency within the population, but often bypass the complexity of genotype-phenotype relationship (for instance by assuming asexual reproduction, clonal inheritance); (2) evolutionary quantitative genetics models (Slatkin 1978; Pease *et al.* 1989; Kirkpatrick & Barton 1997), which integrate the genotype-phenotype map with population demography (e.g., density-dependence) but

where other ecological changes remain independent from the population dynamics; and (3) integral projection models (IPM, Smallegange & Coulson 2013), which use population models classically developed in population dynamics to describe the evolution of continuous characters in a quantitative genetics framework. We purposely do not mention traditional optimisation models, such as stochastic dynamic programming used to represent individual behaviour (e.g., life history decisions) and development (e.g., growth and sexual maturity) and their consequences for population dynamics (Mangel 2015), as these models do not specify the genetic basis of traits, which is mandatory for EEF. The main limitation of the above-listed analytical approaches is that they consider evolutionary and ecological processes (be they deterministic or stochastic) to be homogeneous within groups of individuals (the population or life stages), whereas group composition constantly varies in terms of phenotypes and genotypes, affecting individual decisions, linked to local and instant conditions, and their outcome at the group level (i.e., emerging effects).

	Analytical models	DG-ABMs
Scale	Population	Individual
Population dynamics	Uniform within-populations or within classes	Not uniform, possible structure
Within-population variation	Simplified (2 variants) or Gaussian distribution, no structure	Distribution free, possible structure (e.g. spatial)
Transmission		
Inter-individual interactions	Uniform within-populations	None ↔ Not uniform, explicitly modelled
Trait-fitness relationship	Input, not flexible	Outcome, flexible, allows emerging effects
Management practises	Mean impact, not flexible	On individuals and interactions, allows emerging effects

Figure 1: Different approaches to model eco-evolutionary feedback loops.

This scheme summarises the main differences between two major modelling approaches used to investigate eco-evolutionary dynamics: analytical models on the left and Demo-Genetic Agent-Based

Models (DG-ABMs) on the right. Their main difference is that analytical models consider evolutionary and/or ecological processes to be homogeneous within groups of individuals (the population or life-stages), whereas DG-ABMs can account for phenotypic and genotypic variation in groups of individuals, its effects on individual decisions/traits linked to local and instant conditions, and their outcome at the group level (i.e., emerging effects). In particular, some (although not all) DG-ABMs model interindividual interactions, and their effects on individual fitness, which emerge in part from these interaction

Yet the question of individual heterogeneity and its effects has long preoccupied eco-evolutionary ecologists. For several decades, simulations using agent-based models (ABMs, also called individual-based models or IBMs in ecology) were used to investigate more complex scenarios and explore unexpected EEF, with approaches spreading on a spectrum of complexity well described by DeAngelis & Mooij (2005). On the one side of the spectrum, some ABMs were developed to validate and/or explore the predictions made with analytical models, replace these models and/or eventually nurture their future development. To keep these ABMs as simple as possible, individuals usually have a minimum number of attributes and fitness does not depend on interindividual interactions. For instance, by coupling a niche-based model with individual-based demo-genetic simulations, Cotto *et al.* (2020) investigated the evolutionary constraints related to alpine plant response to a changing climate. The key originality of their approach is to model individuals as spatial points across a complex climatic landscape, where the individual phenotypes are explicitly linked to climatic variables and where the optimal phenotype is prescribed by the niche-based model and varies through time. They use a classical multi-stage life cycle model (from seeds to adults) where individual survival and ultimately fitness increases when the multivariate phenotype is close to the optimal phenotype but is independent of the phenotype of other individuals. This typical top-

down approach aims at extending classic analytical models into more complex domains with the assistance of ABMs.

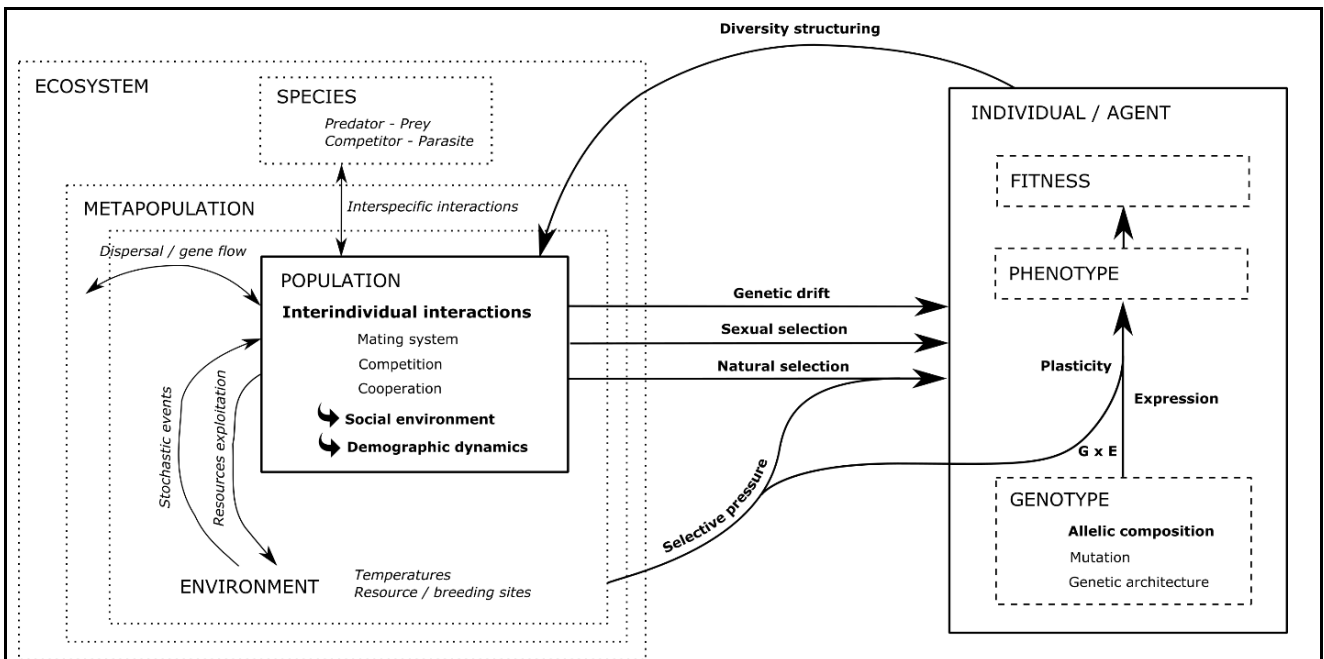
On the other side of the spectrum, some ABMs employ a specific bottom-up approach to fully integrate individual interactions and their outcome over time and space within a population, the result of which will dictate the strength and direction of evolutionary processes at the population level (Huston *et al.* 1988; DeAngelis & Mooij 2005). These ABMs acknowledge that individuals have inherently non-uniform interactions with each other, and that the consequences of the variation in traits mediating interindividual interactions are better described by rule-based simulations than by mathematical models. Accordingly, these approaches depict the interactions between individuals and their effects on individual fitness, accounting for the social context, and observe the resulting dynamics in terms of distributions of heritable traits and demography. We hereafter refer to these ABMs as Demo-Genetic Agent-Based models, DG-ABMs (another possible acronym would be Eco-Genetic ABMs).

DG-ABMs can be defined as individual-based (meta)population dynamics models with heritable trait variation and phenotype-dependent interactions between individuals (Box 2). A key feature of DG-ABMs is that fitness variation emerges mechanically from interactions between individuals (as opposed to assuming an *a priori* fitness function) and gives rise to the evolution of patterns structuring the population diversity and its dynamics (e.g., genetic architecture, spatial genetic structure). Typical examples of emerging fitness variation are spatially structured individual-based models focusing on dispersal evolution (Bach *et al.* 2006; Poethke *et al.* 2007; Kubisch *et al.* 2013). Indeed, these studies demonstrated that genetic structure and kin competition emerge from the spatial design of their DG-ABMs, when coupled with the genetic basis of dispersal and competition (here implicitly accounted for). Hence, dispersal evolves to reduce kin competition and increase inclusive fitness, ultimately

driving back kin structure within populations. This is radically different from assuming a prescribed relationship between traits and fitness, as done in analytical models and some ABMs (e.g., Cotto *et al.* 2020). We argue here that this bottom-up construction of fitness in DG-ABMs provides different and new insights into various fundamental and applied questions in ecology and evolution, and illustrate further our point of view by a review of the literature.

Box 2: An overview of demo-genetic agent-based models (DG-ABMs), and on how they model interindividual interactions.

Conceptual scheme of DG-ABMs (Figure below). Individuals (or agents) are characterised by their phenotypic traits, determined by their genotype, the environment, and interactions between them (denoted G·E). The agents together define the population, hence determining its diversity and structure, where interindividual interactions shape the social environment. This social environment influences population dynamics, which ultimately drives evolutionary processes (drift, selection, gene flow). Fitness variations (e.g., survival, fecundity variation) emerge from different outcomes of interindividual interactions (e.g., mating, competition, cooperation, information exchange) and give rise to evolution of traits via the trans-generational response to selection. This framework, highlighting the feedback loop central to eco-evolutionary approaches, is the core part of DG-ABMs and is identified by solid (units) / dashed (units' properties) line boxes and bold arrows.



Modelling interindividual interactions. ABMs have the general capacity to represent both direct interactions among agents (i.e., when one agent identifies one or more other agents and directly affects them, e.g., by having some kind of contest with them, eating them, or choosing them to mate) and mediated/indirect interactions (when one agent affects others indirectly by producing or consuming a shared resource).

The choice to model these interactions explicitly or implicitly in DG-ABMs depends on the interaction type, the degree of realism/complexity desired, and on the focal, evolvable trait(s) involved in the interaction (see Table 1 for examples of these traits). Direct reproductive interactions are most often explicitly modelled, through variable mate preference or competitiveness among potential mates (e.g., Chevalier *et al.* 2022), or assortative mating for a variable phenological trait (e.g., Soularue & Kremer 2014). This is also the case of direct cooperative interactions, where the mechanisms involved (e.g., in grouping behaviour) are usually explicitly represented (Van Der Post *et al.* 2015; de Jager *et al.* 2020).

Indirect interactions such as competition for resources can be implicitly modelled through density-dependence functions. For instance, most DG-ABMs investigating fisheries-induced evolution assume that increasing density will lead to increasing competition, the competition strength also depending on individual size (Piou & Prévost 2012; Ivan & Höök 2015). By contrast, some DG-ABMs consider competition in an explicit prey-predator (Costa *et al.* 2016) or consumer-resource (Kang & Thibert-Plante 2017) system; in these cases, the level of the resource and the consumption process at each time step are explicitly modelled, and the traits involved in the interaction can be more realistically represented (e.g., gill-raker count in Kang & Thibert-Plante 2017).

DG-ABMs applications: DG-ABMs also offer the opportunity to study eco-evolutionary dynamics at multiple levels of organisation and spatio-temporal scales. At population scale, habitat structuring and variation in the abiotic environment can be included to account for selection, stochastic events and subdivision of the social environment. These models also allow simulations of several populations' dynamics connected through dispersal with potential gene flow, such as in a metapopulation case. At a higher level, community dynamics can be modelled through interspecific interactions between individuals from directly or indirectly interacting species.

Objective and method for the literature review

In their recent review of individual-based modelling of eco-evolutionary dynamics, Romero-Mujalli *et al.* (2019) illustrated how ABMs have been applied to assess organisms' and populations' responses to environmental change, but overlooked whether these ABMs accounted or not for interindividual interactions. Here, we specifically reviewed DG-ABMs in which fitness variation emerges mechanically from interactions between individuals.

To that aim, we searched the Web of Science Core Collection between 1955 and 2022 for various combinations of key-words (Figure S1). A first query using (Individual-based model* OR IBM*) AND (eco-evol* OR demo-genet* OR demogenet* OR ecogenet* OR ecogenet*) returned 138 publications. By using the terms (Agent-based model OR ABM) instead of (Individual-based model* OR IBM*), we obtained 15 publications indicating that the eco-evolutionary community has not appropriated the term ABM despite its broader meaning (e.g., Railsback & Grimm 2019). Of all these 153 publications (Table S1), only 54 included the terms ((interindivid* OR inter-individ* OR individ*) AND interact*). After excluding reviews, technical publications, book chapters, preprint and duplicated studies (Table S2), we retained 120 publications. Finally, as we were interested in studies using a DG-ABM approach, we checked if these 120 remaining publications (1) use an IBM; (2) simulate dynamics over multiple generations; (3) represent (direct or indirect) interactions between conspecific individuals; (4) represent individual variation in the interaction-related trait(s); (5) consider that part of this variation is heritable. With this method, we filtered out 46 additional publications that did not satisfy these five criteria, resulting in a total of 74 publications using DG-ABMs where interindividual interactions affect fitness. Using a snowball approach, we found 14 additional references cited in or citing the 74 selected publications (see Table S3 for the final database). Note that the difficulties we encountered in selecting studies using DG-ABMs with interindividual interactions from the WOS illustrate the need for clearer referencing based on key-words better shared by the community.

Synthesis of the literature review

In the selected 88 studies, competition was by far the most considered interaction (79 studies), followed by reproductive interactions (37 studies) and cooperative interactions (4 studies only). We found 32 studies accounting for two types of interaction simultaneously.

On average, 1.9 traits (between 1 and 19 traits) per study were considered as evolvable. The nature of evolvable trait(s) depended on the interaction type, the species/kingdom considered and the level of generality/realism/precision of the model (following the classification of models properties of Levins -1966). We distinguished eight categories of evolvable traits (Tables 1 and 2): 1) traits related to growth and/or maturation thresholds (35 studies); 2) traits related to mating (12 studies); 3) dispersal traits (12 studies); 4) traits related to cognitive behaviour and information exchange (six studies); 5) traits related to energy acquisition or allocation (six studies); traits related to 6) defence (five studies) or 7) virulence (two studies); 8) and finally, abstract traits - meaning that they do not correspond directly to a measurable trait - generally related to competitive ability or/and assortative mating (17 studies). We found seven studies considering two types of traits simultaneously. While some of these traits directly mediate interindividual interactions (e.g., mating traits for reproduction, behavioural traits for cooperation), most of them indirectly impact interactions. For instance, dispersal traits or movement preferences are often associated with avoidance of competition and/or predation, or mate search for reproduction (Travis *et al.* 2012; Fronhofer & Altermatt 2017). Traits related to growth, maturation and energy acquisition or allocation, influence individual size, which often plays a major role in the outcome of competition.

Table 1: Interindividual interactions and associated evolvable traits modeled in DG-ABM

To illustrate the categories of traits considered as evolvable in the reviewed DG-ABMs, we listed some examples depending on the interaction type considered (IT): competition (C), reproduction (R) or cooperation (Coo).

IT	Evolvable traits Category	Examples	Examples of references (Species/kingdom)
C	1) growth/maturation	Size at emergence	Fielding 2004 (grasshopper); Ayllón <i>et al.</i> 2016, 2018 (trout)
		Threshold for size at migration	Piou & Prévost 2012, 2013 (salmon)
		Growth rate	Kang & Thibert-Plante 2017 (alewife); Moya-Laraño 2011 (generic); Travis <i>et al.</i> 2010 (plant)
	2) abstract trait	Competitive abilities	Gascuel <i>et al.</i> 2015; Pontarp <i>et al.</i> 2015; Ward & Collins 2022 (all generic for species community)
		4) dispersal trait	Prospecting of habitat quality
	5) behaviour	Dispersal distance	LaRue <i>et al.</i> 2019 (sea rocket); Leiding <i>et al.</i> 2021 (plant)
		Movement preference	Hrycik <i>et al.</i> 2019 (perch)
	6) energy, allocation	Drifting	Mazzucco <i>et al.</i> 2015 (shrimps)
		Functional traits related to energy acquisition	Ivan & Höök 2015 (perch); Mollet <i>et al.</i> 2016 (plaice)
	7) defence	Toxin production	de la Peña <i>et al.</i> 2011 (plant-herbivores)
8) virulence		Abstract defence	Costa <i>et al.</i> 2016; Urban <i>et al.</i> 2019 (generic)
	Pathogen virulence	Papaix <i>et al.</i> 2018; Rimbaud <i>et al.</i> 2018 (plant pathogen)	
R	1) growth/maturation	Threshold for size at maturity	Ayllón <i>et al.</i> 2016, 2018 (trout); Piou & Prévost 2012, 2013 (salmon); Kane <i>et al.</i> 2022 (trout)
		Slope/intercept of the maturation reaction norm	Dunlop <i>et al.</i> 2007 (bass)
	3) mating	Selfing or self-incompatibility	Kirchner <i>et al.</i> 2006; Katsuhara <i>et al.</i> 2021 (plant)
		Mate choice (preference, competitiveness), mate search	Berec <i>et al.</i> 2018; Chevalier <i>et al.</i> 2022 (generic); Labonne & Hendry 2010 (guppy); Nathan <i>et al.</i> 2019 (trout)
Coo	2) abstract trait	Mutualistic or antagonistic trait	Maliet <i>et al.</i> 2020 (generic)
		5) cognitive behaviour	Grouping, schooling behaviour
	Attachment density	de Jager <i>et al.</i> 2020 (mussel)	

These evolvable traits are at the core of the EEF loop in DG-ABMs, since fitness variation emerges from interactions among individuals that differ in these traits, giving rise to

population dynamics in terms of both distribution of evolvable traits and demography. We distinguished five main types of EEF in the reviewed DG-ABMs (Table 2). We found 16 “Ecology-focused” DG-ABMs, with a high level of realism in the demographic and ecological processes, and incorporating a “dose” of evolutionary processes to gain a better understanding of the ecological/demographic behaviour. In these DG-ABMs, evolvable traits were most often growth/maturation traits, but six other trait categories were considered. Then, we found 19 “Microevolution-focused” DG-ABMs, with a high level of generality in the evolutionary processes, and incorporating a “dose” of demographic and ecological processes to gain a better understanding of the evolutionary behaviour at a contemporary timescale. Similarly, there were also 13 “Macroevolution- focused” DG-ABMs, dedicated to the understanding of speciation at a macroevolutionary time scale. In these “Micro- or macroevolution-focused” DG-ABMs, the evolvable trait was most often abstract, but mating traits were also often considered. Then, we identified 24 “Management- focused” DG-ABMs, used to address how management practices interfere with the EEF loop with a high level of precision; in these DG-ABMs, evolvable traits were most often growth/maturation traits. Finally, we found 16 “Spatial-focused” DG-ABMs, used to investigate EEF in a spatially explicit context (e.g., metapopulation). These DG-ABMs investigated in particular the evolution of dispersal traits.

Table 2: Association between the category of evolvable traits considered in each DG-ABM, and the type of eco-evolutionary feedback considered.

Trait category	Type of eco-evolutionary feedback					
	Ecology-focused	Microevolution-focused	Macroevolution-focused	Management-focused	Spatial-focused	Number of studies
Growth/Maturation	5	2	3	16	3	29
Abstract trait	2	7	8			17
Dispersal	2				9	11
Mating	2	5		1		8
Cognitive behaviour	2	1	1		2	6
Defence	1	2			1	4
Energy acquisition or allocation	2	1		1		4
Virulence				2		2
Mating & growth/maturation			1	2		3
Mating & Energy acquisition or allocation		1				1
Growth/maturation & Defence				1		1
Growth/ maturation & Dispersal					1	1
Growth/ maturation & Energy acquisition or allocation				1		1
Number of studies	16	19	13	24	16	88

Another characteristic of DG-ABMs is the type of inheritance framework used to model genetic variation in the evolvable traits. We found that 73% of the studies used a Mendelian inheritance process either in a population genetic framework (one locus, possibly multi-allelic, which directly determines the phenotype) or combined with a quantitative genetic framework (several loci, together with the environment, which govern trait variation). Besides, 24% of the studies used an infinitesimal quantitative genetic framework (where each offspring inherits the mean of the two parent's genetic values), and two studies (3%) tested for population versus quantitative genetic framework. Note that our definition of DG-ABM is larger than the one suggested by some authors (e.g., Frank & Baret 2013), who proposed to

reserve the term “eco-genetic” to models based on a quantitative genetics framework, and the term “demo-genetic” to models based on a population genetics framework.

Beyond these general typologies, we illustrate below the main applications of the reviewed DG-ABMs, through selected examples.

DG-ABMs to better understand eco-evolutionary feedback loops

Accounting for variable within-population interindividual interactions in a bottom-up approach allows DG-ABMs to better investigate the emergence of fitness variation resulting from several complex eco-evolutionary processes and the interactions between them. Accounting for the stochastic and context-dependent outcomes of competitive, cooperative, or reproductive interactions can change the predicted evolution of life-history traits compared to an approach where the relationship between traits and fitness is prescribed. Below, we emphasise relevant studies from our literature review which investigate these three types of interaction.

We start with examples of DG-ABMs considering explicit **competitive** interactions within species. Fielding (2004) investigated competition in grasshoppers and showed that contrasted optimal values of life history traits can emerge from different types of localised interindividual interactions, i.e., exploitative or size-based competition. In their DG-ABM of trout population, Ayllón *et al.* (2016) observed the emergence of different eco-evolutionary outcomes due to explicit competitive interactions for food in a changing environment. These two DG-ABMs with explicit competitive interactions were built from well-tested demographic models, and additionally considered that the same traits (size at emergence and maturity size threshold) could evolve and interact with the spatial distribution of food resources to shape

population dynamics. Most often in the reviewed DG-ABMs focusing on single species adaptive dynamics, competition is implicitly considered, e.g., through a density-dependence function. In a perch species, Ivan & Höök (2015) showed variable patterns of energy allocation along individual ontogeny, resulting from the interplay between plastic and adaptive responses to selection and density-dependent competition for food. Using a DG-ABM representing competition among individuals choosing different life-history tactics, Piou & Prévost (2012, 2013) showed that climate change may modify salmon population dynamics through plastic responses of individual size. These two DG-ABMs acknowledge the main role of individual size on competition, and incorporate both genetic and plastic variation in this trait to gain a better understanding of the adaptive population dynamics in future, changing environments.

Integrating behavioural interactions between individuals and EEF is logically critical to understand the evolution of sociality and **cooperation**. Van Der Post *et al.* (2015) investigated how grouping, a taxonomically widespread social process, co-evolved with two cooperative social behaviours: anti-predator vigilance and foraging. In a simulation experiment where behavioural processes were specified through 19 variable traits, but not the cost and benefits of each decision strategy, they showed eco-evolutionary interactions between group size and vigilance with an evolutionary trajectory towards bigger groups and less vigilance, eventually leading to fission into small groups with high vigilance and back. Accounting for heritable interindividual differences and environmental heterogeneity in resource distribution, Reuter *et al.* (2016) were able to relate landscape structuration to the evolution of schooling behaviour and collective foraging in fish. Although these studies mostly focused on how cooperation can emerge in models where costs and benefits are not explicitly specified but

related to other behavioural traits, reverse strategy, where cooperation is the evolvable trait, could also be used to investigate adaptive dynamics.

Reproductive interactions are an obvious major driver of demographic dynamics, and “Ecology-focused” DG-ABMs are particularly suitable to investigate this issue in an eco-evolutionary framework. For instance, to explore how mating behaviour and population size jointly affect fitness components or population growth rate through Allee effects, Berec *et al.* (2018) considered the rate of mate search as evolvable and found different optimal values of search rates for populations at different densities, resulting in lower Allee thresholds in populations kept at lower densities. DG-ABMs are also relevant to examine the interplay between demographic processes and the mating system when self-incompatibility (Kirchner *et al.* 2006) or sterility (Nonaka & Kaitala 2020) occur as a direct consequence of the genotype.

Reproductive interactions are also known to drive evolutionary dynamics (Maan & Seehausen 2011), and explicit representation of mating interactions is important as sexual selection can sometimes oppose natural selection (Labonne & Hendry 2010), or eventually reinforce it (Soularue & Kremer 2014). Mate choice strongly depends on the population structure, making the outcome challenging to predict yet rarely random (Klug & Stone 2021). DG-ABMs, by allowing to represent explicitly sexual interactions, are particularly adapted to explore the evolution of traits considering the dynamic aspects of mating systems, such as when sexual preference and competition over mating partners occur, while still accounting for natural selection (Nathan *et al.* 2019; Chevalier *et al.* 2022). In this context, growth traits, or traits related to life-history decisions such as migration or maturation, are often chosen as key traits to jointly consider size-dependent survival and reproductive interaction and their possible interactions (Piou *et al.* 2015; Ayllón *et al.* 2019). Another application is the

investigation of sexual dimorphism, which can arise when a given trait is subject to different selection pressures in males vs females (or even opposing pressures in the case of sexual conflict), but has a shared genetic basis between the sexes. Höök *et al.* (2021) showed how sex-specific plasticity for size could evolve by looking at perch evolutionary response to environment. Kane *et al.* (2022) showed that optimal migration propensity differed among males and females in trout, and that populations could adapt to environmental change across a range of intersex genetic correlations for migration propensity, which influence the magnitude of sexual conflict.

Extending in space, time and levels of organisation

In most examples detailed above, eco-evolutionary dynamics are modelled within a non-spatially explicit population. However, the spatial arrangement of habitats shapes animal movements or gametes propagation, and therefore also shapes social interactions and sexual networks (He *et al.* 2019). Since they allow fine-scale explicit representation of habitats as well as individual movements, DG-ABMs are well suited to represent **spatial evolutionary dynamics**. Focusing on the evolution of dispersal, Fronhofer & Altermatt (2017) showed how EEF can emerge from a simple spatially-explicit DG-ABM. Depending on network topology and connectivity, variable evolutionary stable dispersal strategies emerged from their model via kin competition, and lead to EEF by changing back the network's demography and genetic structure. Hrycik *et al.* (2019) explored the importance of environmental cues in perch vertical movement. By allowing movement rules in response to these cues to evolve, they illustrated the role of DG-ABMs in determining appropriate movement rules in spatially-explicit ecological modelling. Travis *et al.* (2010) used a mechanistic DG-ABM approach to model the evolution of seed dispersal in plant populations, accounting for likely trade-offs between

traits in a patchy landscape. Additionally, sexual selection can determine the reproductive success of immigrants in populations and thus the strength and direction of demo-genetic consequences of dispersal (e.g., demographic rescue, evolutionary rescue vs gene swamping). For instance, Soularue & Kremer (2014) highlighted the major importance of gene flow and assortative mating in shaping the genetic differentiation between populations in a heterogeneous environment.

Interactions between conspecific individuals are at the core of DG-ABMs. In addition, considering explicitly higher levels of organisation (e.g., community level) to represent **interspecific interactions** may ultimately change the evolutionary outcomes expected from single species systems (Weber *et al.* 2017; Terhorst *et al.* 2018). We found examples of such multispecies DG-ABMs used to investigate mating interactions: for instance, using an ABM in which two plant species share the same pollinators, Katsuhara *et al.* (2021) highlighted that the evolution of selfing without pollinator assistance (autonomous selfing) may increase population growth rates of inferior competitors and consequently favour long-term coexistence via an evolutionary rescue. Furthermore, McDonald *et al.* (2019) showed that the strength of intraspecific competition for mates may result from sexual interactions with heterospecifics, which may interfere with sexual selection (i.e., interspecific reproductive interference).

Most of the reviewed multispecies DG-ABMs focused on competitive interactions, in an explicit prey-predators' or community context. For instance, Kang and Thibert-Plante (2017) illustrated that considering trophic interactions and the genetic basis of functional traits within a single model could improve the understanding of evolutionary morphological changes in fish. Hillaert *et al.* (2020) showed that in a fragmented habitat, the presence of

predators selects for increased herbivore movement and hence larger herbivore size. Demogenetic models of plant-virus interactions allowed to investigate the emergence of plant viral genotypes breaking down plant qualitative resistance genes (Fabre *et al.* 2009). Ecological interactions at the community level may drive selection within species, and selection may affect in return the processes of species assembly at a community scale (Leidinger *et al.* 2021). Finally, as multispecies DG-ABMs represent both intra-and interspecific complexity, they are especially suited to address macroevolutionary consequences of interspecific interactions, such as speciation (Gavrilets *et al.* 2007; Weber *et al.* 2017). We found several examples of macroevolution-focused DG-ABMs developed to investigate adaptive radiation, i.e., the rapid diversification of a single lineage into many species with a great diversity of ecological strategies (Gascuel *et al.* 2015; Pontarp *et al.* 2015; Ward & Collins 2022). These models generally consider a limited number of abstract, phenotypic traits reflecting the competitive ability of the focal individual with all the other individuals of the local patch. The distance between these ecological phenotypes within a patch drives exploitative competition, while heritable variation of the ecological phenotype fuels the processes of local adaptation and speciation.

Overall, it appears that DG-ABMs have a large potential to address fundamental eco-evolutionary questions accounting for multiple drivers of fitness, and are increasingly used in an integrative way, allowing effects to flow up and down between organisation levels.

DG-ABMs to assist management strategies

Another key feature of DG-ABMs is their capacity to model the effects of management practices on individuals and their interactions, together with that of other eco-evolutionary processes. Hence, by allowing emerging effects, DG-ABMs can also be efficient prospective

tools to elaborate and assess management strategies. When management consists of **demographic control of populations**, in particular through individual phenotype-based choices, it can deeply impact all demographic processes and population genetic composition, and therefore the intensity and direction of the evolutionary processes (Lefèvre *et al.* 2013). For example, selective fishing (or harvesting) directly affects competition among surviving fish (or trees), while genetic composition determines optimal fishing (or harvesting) patterns. In particular, different DG-ABMs were used to understand how selective fishing can affect the demography and evolution of fish populations (fisheries-induced evolution), through cascading and sometimes counterintuitive effects on population demographic structure, growth and maturation thresholds (Wang & Höök 2009; Piou *et al.* 2015; Wang *et al.* 2017; Ayllón *et al.* 2018). By simultaneously modeling the plastic and genetic responses of individuals, DG-ABMs can also disentangle the role of selective fishing and environment in the observed and predicted population declines and phenotypic changes (Piou *et al.* 2015).

When evolutionary dynamics and **land use planning decisions** are linked, DG-ABMs also represent valuable decision support tools. For example, Papaix *et al.* (2018) and Rimbaud *et al.* (2018) used a spatially explicit demo-genetic model to assess the joint effect of crop cultivar deployment strategies in space and time and key pathogen life-history traits on epidemiological dynamics, resistance durability and long-term evolutionary control. Using a DG-ABM, Mims *et al.* (2019) found strong effects of spatial connectivity on demo-genetic outcomes in reintroduced bull trout populations, and allowed identification of watershed areas with higher persistence probabilities.

In the case of **hybridization** between native/wild and introduced/domesticated gene pools, DG-ABMs allow to study the impact of management on the dynamics of crossing within

and between gene pools, which depends on differential social interactions (e.g., mating preference) and genetic performances (e.g., local adaptation) between gene pools (Castellani *et al.* 2015; Nathan *et al.* 2019). In this context, DG-ABMs are an effective means of developing genetic enrichment strategies in a prospective approach (which genetic resources and which deployment modalities for which risks?), and conversely of evaluating strategies aimed at preserving the local gene pool from unwanted introgression.

In these different case studies, DG-ABMs offer a relevant framework to evaluate the short- and long-term evolutionary costs and benefits of management actions and to assess potential trade-offs between them. For example, they allow to address the issue of exploiting a population or a metapopulation (e.g., fishing, wood production) while preserving its genetic value and diversity, or to determine how to minimize the risks of demo-genetic collapses of populations facing climate change. Furthermore, by controlling the social context of populations, management drives the overall ecological processes and thus affects biotic and abiotic stressors, the susceptibility of populations to these stressors, and selection intensity (Jactel *et al.* 2009).

Taking advantage of ABMs for DG-ABMs

The above-listed examples from our literature review illustrate the diversity of interindividual interactions, adaptive traits and ecological processes that can be investigated using DG-ABMs. This diversity is a strength, but requires active strategies to better identify possible links between similar models developed to answer different questions, and to structure the community of developers and users of these models. Identified as agent-based models, DG-ABMs can benefit from multiple advances in the ABM community. The flexibility of the approach ranges from very simple and generic models to very complex and specific

models, depending on model assumptions and objectives (Edmonds & Moss 2005). A wide panel of tools and methodologies are available to explore DG-ABMs (Thiele *et al.* 2014). The exponential increase of genomic databases should help in the calibration/validation of DG-ABMs (Rudman *et al.* 2018). The use of description protocols such as Overview, Design concepts and Details (ODD) protocol ensures the replicability and enhances the understanding of the models (Grimm *et al.* 2020). The TRACE framework (Grimm *et al.* 2014) is also a powerful tool for planning, documenting, and assessing model development, analysis and application. Software for ABM development have increased in simplicity, quality, speed of computation and reliability and allow sharing pieces of code easily (Dufour-Kowalski *et al.* 2012); in particular, quantitative genetic libraries can be plugged into existing population dynamic models to describe the genetic architecture of adaptive traits (e.g., “Genetics” library in CAPSIS Dufour-Kowalski *et al.* 2012; Oddou-Muratorio & Davi 2014). Software for complex model exploration have been proposed (Reuillon *et al.* 2013). Complex and multi-authored models may use modelling notebooks to keep trace of all steps of conceptualisation, model development, implementation and exploration in order to enhance the confidence of end-users of DG-ABMs in the management communities (Ayllón *et al.* 2021). Finally, the publication of model codes on specific dissemination platforms is encouraged in the ABM community (e.g., <https://www.comses.net/codebases/>). All these recommendations should benefit the development of DG-ABMs.

Intrinsically, DG-ABMs conception requires a multidisciplinary approach integrating multiple levels of knowledge and can be used in interdisciplinary research projects as a tool of interaction among disciplines. Agent-based models are also used as frontier objects in several contexts (Le Page & Perrotton 2017; Reilly *et al.* 2021). As such, DG-ABMs are

important tools in interacting with management or other end-user communities that need to incorporate evolutionary processes in their decisions. Although this has not been done so far, DG-ABMs could even be developed as part of a participatory modelling approach (Le Page *et al.* 2012) to integrate the knowledge of a diverse community of experts that need to manage constantly evolving ecosystems. Finally, they should become essential to adaptive management with an evolutionary perspective (Groot & Rossing 2011).

Conclusion

In complement to the analytical models traditionally employed by evolutionary ecologists to investigate EEF loops, this review puts forward DG-ABMs, which are individual-based (meta)population dynamics models with heritable trait variation and phenotype-dependent interactions between individuals. Our literature review illustrates how the bottom-up construction of fitness in these DG-ABMs allows them to provide new insights into various fundamental and applied questions in ecology and evolution.

Previous reviews of the literature have indicated that ABMs in general are not used to address general questions in ecology and evolution, but have a more “narrow” or “pragmatic” scope (DeAngelis & Grimm 2014). We advise modellers working on eco-evolutionary processes to carefully consider the benefits of accounting for the effects of interactions between individuals on fitness in their approach, since it might significantly affect the direction and magnitude of evolution. This is true for theoretical investigations as well as for more applied objectives, since these eco-evolutionary mechanisms also operate on rather short time scales (a handful of generations). Using a dedicated term - such as DG-ABM - would facilitate a distinction between categories of modelling approaches, highlighting the specifics

of eco-evolutionary models accounting for interindividual interactions and their variations, and the potential differences in their respective predictions.

Author contribution

All authors contributed equally to the conceptualization of the ideas developed in this study, and to the initial review and synthesis of the literature. Hence, the first five authors (A.L., V.F., D.F., C.V., and L.D.) should be considered as co-first authors, while the five last authors (J.L., M.B. F.L., C.P, S.O-M.) should be considered as co-senior authors. The doctoral students (A.L., V.F., D.F., C.V., and L.D.) wrote the first draft of this manuscript and designed the figures. A smaller group (A.L., L.D., M.B., F.L., S.OM) took on the second literature survey required by the reviewers. All authors reviewed, edited and approved the final manuscript. Acquisition of funds: J.L and C.P.

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3. Luberon2, un modèle démo-génétique pour l'étude des interactions entre la gestion et les processus évolutifs en forêt

Mes travaux tirent parti du modèle de couplage démo-génétique individu-centré Luberon2 développé au sein de l'URFM – INRAE sur la plateforme de modélisation Capsis. Pour une description complète de la structure, des paramètres initiaux et du fonctionnement général de Luberon2, se référer au manuel d'utilisation disponible en ligne⁵ et à l'article 2 de ce manuscrit de thèse.

Initialement, Luberon2 résulte du couplage d'un modèle de dynamique forestière cèdre avec un modèle de génétique quantitative. Chaque composante démographique du modèle a été calibrée empiriquement (Courbet, 2002 ; Bertrand, 2004 ; Klein, comm. pers.), et le modèle de génétique quantitative permet de reproduire la variation phénotypique observée au sein d'un peuplement (Dreyfus et al., 2004 ; Seynave & Pichot, 2004). En tant que modèle DG-ABM, la boucle d'évolution annuelle de Luberon2 correspond à une boucle de rétroaction éco-évolutive où les valeurs génétiques individuelles déterminent la performance des arbres en termes de croissance, de reproduction et de survie, tandis que le modèle de dynamique forestière détermine la structure du peuplement à partir des performances individuelles ; la structure du peuplement étant elle-même une condition de l'environnement et de la pression de sélection de la diversité génétique. Des outils de simulation d'interventions sylvicoles systématiques ou sélectives en fonction de la taille de l'arbre, dont plusieurs ajoutées dans le cadre de mes travaux, peuvent être utilisés pour modifier la composition et la structure du peuplement. L'évolution génétique du peuplement résulte mécaniquement des processus démographiques, notamment la mortalité par sur-densité (auto-éclaircie) et la régénération, et des interventions sylvicoles dans un contexte de variation interindividuelle. L'auto-éclaircie élimine préférentiellement les arbres les moins compétitifs, c'est-à-dire les plus petits. Lors de la régénération, les gros arbres produisent plus de gamètes.

Luberon2 permet une utilisation dans un environnement graphique interactif (Fig. 3) ou dans un mode script, développé dans le cadre de mes travaux, où un fichier de commande

⁵ Godineau, Fririon et al., 2022 : https://capsis.cirad.fr/capsis/help_en/luberon2

donne les instructions pour : (i) le fichier input du peuplement initial à utiliser, (ii) l'enchaînement des étapes à simuler avec leurs options et (iii) les types de sorties.

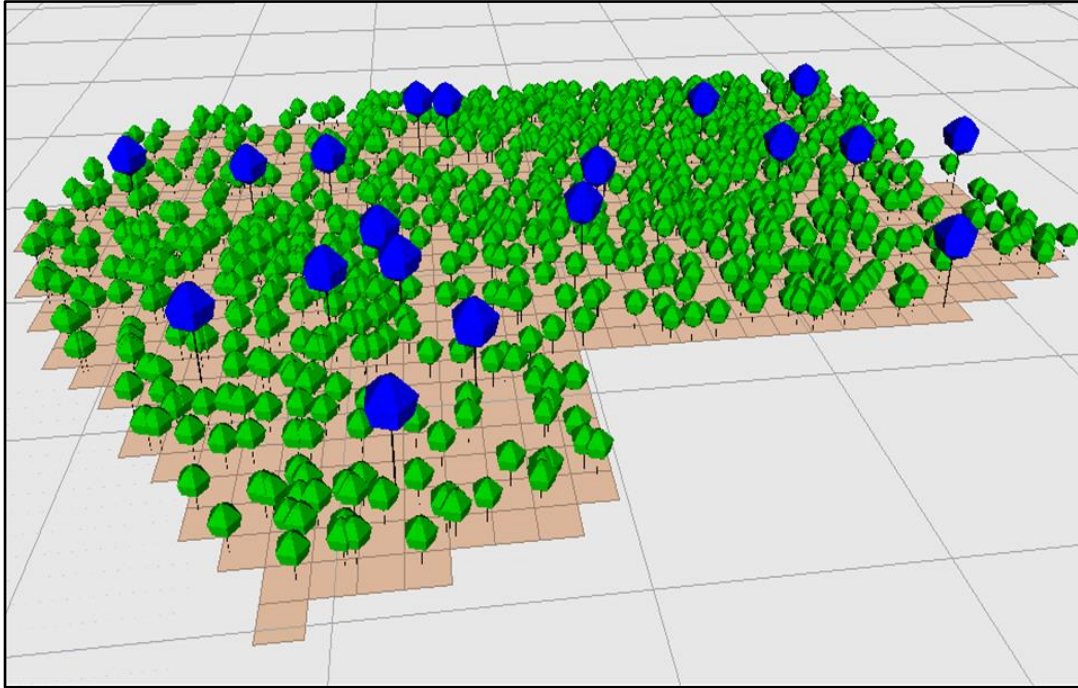


Figure 3. Visualisation 3D avec Luberion2 en mode fenêtre interactive d'une parcelle forestière. Ici, le peuplement a été régénéré naturellement. Les semenciers, en bleu, sont encore présents. Leurs descendants sont représentés en vert.

V - Luberon2 comme preuve de concept de l'approche par modélisation démo-génétique en forêt

1. La question de la validation du couplages démo-génétiques de Luberon2

Nous n'avons pas aujourd'hui de dispositifs expérimentaux permettant de valider empiriquement les prédictions d'impacts génétiques de différentes opérations sylvicoles. Ceci nécessiterait des dispositifs basés sur une évaluation génétique individuelle sur plusieurs générations d'arbres. En dehors de ma thèse, parallèlement aux approches de modélisation, on peut imaginer la mise en place de tels dispositifs pour tester différentes options sylvicoles à long terme (Lefèvre et al., 2014), mais cela prendra du temps. En parallèle, il serait possible de tenter de reconstituer *a posteriori* des équivalents de tels dispositifs à partir de peuplements dont les arbres fondateurs sont encore aujourd'hui présents, comme c'est le cas pour le peuplement de cèdres du Petit Luberon (Vaucluse, France). Toutefois, cette situation reste complexe à traiter du fait du manque d'archives sur l'installation du peuplement et les diverses interventions ayant eu lieu jusqu'à maintenant. Pour ces différentes raisons, l'évaluation de la pertinence des résultats de simulation démo-génétique est rapidement apparue comme un défi. Quatre niveaux de vérification de la pertinence des résultats de simulations d'un modèle couplant dynamique forestière et génétique avaient été identifiés : (i) la calibration de chacune des composantes du modèle (modèles de croissance, de fécondité, de dispersion, base génétique des caractères, diversité génétique intra-peuplement, régime de perturbation) sur des données empiriques ou des attendus théoriques ; (ii) les effets de la prise en compte de la variabilité génétique individuelle sur les prédictions dendrométriques du modèle ; (iii) la pertinence des prédictions génétiques des simulations en l'absence de données expérimentales auxquelles se rattacher ; (iv) la sensibilité du modèle aux valeurs choisies des différents paramètres dans les différentes parties du modèle. Seul le premier niveau de vérification avait été réalisé avec Luberon2. J'ai en particulier étudié comment les processus démo-génétiques du modèle restituent les attendus théoriques des processus évolutifs de sélection, et comment les prédictions du modèle de croissance sont affectées par différents effets du couplage.

2. Article 2 (en cours de finalisation). A demo-genetic model shows that non-selective silviculture and disturbances affect natural selection in tree populations

Le contenu de cette section correspond à un article en cours de finalisation visant d'une part, à présenter Luberon2 comme un exemple de modèle couplé démo-génétique en posant la question de la validation d'un tel couplage et, d'autre part, à comprendre les différents mécanismes par lesquels des interventions sylvicoles et des perturbations naturelles non sélectives interfère avec la sélection naturelle chez le cèdre. Le caractère étudié est la vigueur, c'est-à-dire le potentiel de croissance individuel. Des indicateurs du potentiel d'adaptation pertinents dans l'évaluation des processus démo-génétiques en forêt tels que le taux de mortalité, le taux d'évolution, les moyennes et variance génétiques, ou encore les performances de croissance du peuplement ont été identifiés et analysés. En outre, cette étude constitue une analyse de sensibilité pour l'évaluation du couplage démo-génétique de Luberon2. Il s'agit d'un travail collectif avec l'ensemble des personnes ayant participé au développement de Luberon2. En tant que co-premier auteur, j'ai participé au développement du modèle, conçu et exécuté le plan de simulation, réalisé les analyses, réalisé les figures et participé à la rédaction de l'article dans son ensemble.

Les résultats montrent que la sélection naturelle dépend étroitement (i) de la compétition interindividuelle qui se manifeste notamment par le processus de mortalité par auto-éclaircie et (ii) du processus de reproduction sexuée, alors que les grands arbres sont moins sensibles à la compétition et produisent une plus grande quantité de gamètes. En réponse à la sélection, on observe une augmentation rapide de la vigueur et des performances de croissance du peuplement appréciable dès la première génération. En outre, les résultats montrent qu'une gestion intensive, i.e. nombreuses éclaircies systématiques, en réduisant la compétition, limite drastiquement la capacité d'adaptation des peuplements, fait aggravé en présence de perturbations naturelles non sélectives. Les résultats montrent également que le raccourcissement du cycle sylvicole augmente les opportunités de sélection sur la fertilité et concentre la période d'exposition à la compétition à un stade plus précoce où elle peut avoir un impact évolutif élevé. Les taux d'évolution observés sont dans une gamme empirique réaliste, ce qui représente un élément fort de validation du modèle.

A demo-genetic model shows that non-selective silviculture and disturbances affect natural selection in tree populations

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Abstract

Biological production systems and conservation programs benefit from and should care for evolutionary processes. Developing evolution-oriented strategies requires knowledge of the evolutionary consequences of management across timescales. Here, we used an individual-based demo-genetic modeling approach to study the dynamic feedback between silviculture and the genetic evolution of forest tree populations.

The model combines growth, competition and regeneration processes, which jointly drive survival and mating success, with genetic variation of quantitative traits related to these processes. The evolutionary rates predicted by the coupled demo-genetic model for a growth-related trait, vigor, in various management and disturbance scenarios fit in the range of empirical estimates found in the literature for plant and animal populations. We also analyzed the sensitivity of the model to the assumptions made on the genetic architecture of the trait of interest.

Using this model to simulate non-selective silviculture and disturbance scenarios over four generations of trees, we characterized and quantified the effect of thinning frequencies and intensities, and length of the management cycle, on viability selection driven by competition and fecundity selection. The thinning regimes had a drastic long-term effect on the evolutionary rate of vigor over generations, potentially reaching 86% reduction, depending on management intensity, cycle length and disturbance regime. The genetic variance eroded by viability selection within each generation was restored at each reproduction step, resulting in low long-term impact of management on the variance across generations, despite possible short-term impact within generation. The

comparison among silviculture and disturbance scenarios was qualitatively robust to the assumptions on the genetic architecture of the trait.

Thus, the evolutionary consequences of management do not only result from specific anthropogenic selection, not considered here, but also more generally from the interference between human interventions and natural evolutionary processes.

Keywords

demo-genetic agent-based model; evolutionary rate; microevolution; eco-evolutionary feedback; forest

1. Introduction

Eco-evolutionary processes received increasing attention in the context of the current rapidly changing environment (Hendry 2017), and human interventions interfere with those eco-evolutionary processes. In natural and artificial populations managed over multiple generations, the human interventions on populations' composition, structure and dynamics have multiple impacts on the evolutionary drivers, i.e. genetic drift, selection and gene flow. The consequences of human interventions on the genetic diversity and evolutionary trajectory emerge from the joint effects of these multiple drivers. Interference between management and eco-evolutionary processes mainly proceeds from three mechanisms, which can be combined. Firstly, evolutionary consequences result from the demographic impacts of management on population size or other demographic rates, *e.g.* demographic reinforcement in conservation programs (Seddon et al., 2014), or, reversely, reduction of the effective population size leading to genetic erosion in harvested populations (Allendorf et al., 2008), or, indirectly, large-scale release of translocated individuals changing population composition and structure with possible adverse genetic consequences (Laikre et al., 2010). The second mechanism results from the management of the genetic diversity itself, *e.g.* genetic rescue in conservation programs (Whiteley et al., 2015), or directional anthropogenic selection pressure in harvested populations (Coltman et al., 2003). The third mechanism results from the impacts of management on populations' structure and dynamics, which may affect the natural evolutionary processes: this type of evolutionary impact of management has received less attention (but see Bouffet-Halle et al., 2021). In this work, we present a simulation tool to study all these interferences in forest tree populations, and we use it more specifically to characterize and quantify the role of silviculture as a potential "regulator" of natural selection regardless of any direct anthropogenic selection. Understanding this role is needed to develop a stewardship approach of evolutionary management that benefits from and cares for natural evolutionary processes (Mathevet, 2018).

Predicting short- and long term evolution in managed populations is highly challenging, particularly for long-lived species like trees because : (i) longer life cycles offer more opportunities for stochastic disturbance events; (ii) the intensity of evolutionary drivers (*e.g.*, viability or fecundity selection) may change over time within generation in response to disturbance and management interventions; (iii) the short-term, within generation response to selection does not linearly translate into long-term, among-generation evolutionary rates; and (iv) management decisions may be challenged by trade-offs between short- and long-term objectives, *e.g.* choice of the genetic material for afforestation when there is trade-off between adaptation to current vs future environmental conditions. However, knowledge on the mechanisms of evolutionary impact of management and, whenever possible, a quantitative assessment of these impacts are urgently needed to elaborate

exploratory scenarios covering a wide range of plausible outcomes to guide management decisions in the context of global change (IPBES, 2016). In the case of forest management, a general framework characterizing the pathways from silviculture interventions to their evolutionary impacts has been proposed (Lefèvre et al., 2014), opening the way towards their integration in adaptive forest management strategies with a combined objective to speed-up adaptation to environmental change while preserving genetic diversity to cope for an uncertain future. However, the quantitative assessment of those impacts of silviculture, in the short and the long term, remains a research question, particularly for what concerns the evolution of fitness-related traits.

Demo-genetic agent-based models (DG-ABM), defined as individual-based population dynamics models with heritable trait variation and phenotype-dependent interactions between individuals, proved to be an efficient way to simulate evolutionary scenarios that account for interactions between management and natural eco-evolutionary processes (Coulson et al., 2006; Lamarins et al., 2022). Following this approach, we developed a forest dynamics model with heritable trait variation, named *Luberon2*, to simulate the evolutionary processes in monospecific stands with silviculture and stochastic disturbance. In this model, natural selection is dynamically driven by individual tree growth in relation with survival and mating success. Hence, *Luberon2* is typically designed to investigate the genetic evolution of traits related to growth, survival or reproduction over a few generations.

A major challenge in such predictive modeling exercise is the validation of the simulated evolutionary dynamics. *Luberon2* combines a forest growth and demographic model with a quantitative genetic model of individual variation and heredity. Growth and demographic processes are individually calibrated on empirical data, and a finite quantitative trait loci (QTL) genetic model is used to reproduce observed within-stand phenotypic variation and heredity. Although each of these components can be separately validated, assessing the validity of joint predictions when all processes are combined remains challenging for three reasons. Firstly, introducing genetic variation, *i.e.* non-stochastic and inherited inter-individual variation, may affect the predictions of the forest growth and dynamics and progressively deviate from the previous calibration domain after several generations. Secondly, the coupled model aims at exploring complex eco-evolutionary feedbacks that may result in non-monotonous genetic trajectories hardly comparable to empirical data. Thirdly, multiple levels of stochasticity in the demographic and inheritance processes may result in blurred predictions. To validate predictions of such coupled models, multigeneration demographic and genetic records are sometimes available in managed population systems (*e.g.* Thomas et al., 2016; Mathieu-Bégné et al., 2019), but not yet available for long-lived organisms like trees. However, if the predictions of demo-

genetic models cannot be compared to multi-generational empirical data for trees, it remains possible to compare the predicted evolutionary rate with empirical estimates. Here, we used the standard measure of evolutionary rate proposed by Gingerich (1993), i.e. the average evolution of a trait per generation in units of phenotypic standard deviations, to compare the evolutionary rate predicted by Luberon2 with reviews of empirical estimates in wild populations (Bone & Farres, 2001; Hendry et al., 2008; Gingerich, 2009).

This study investigates the rate of evolutionary change of a growth-related trait, vigor, defined as the deviation of individual diameter increment to the baseline prediction by the tree growth model, under quantitative genetic and environmental control. We first characterized the natural process of indirect selection on vigor through competition and mating success, both related to tree diameter, in scenarios without silviculture and management, considering various quantitative genetic backgrounds. We also quantified the feedback effect of the evolution of vigor on forest productivity. Then, we simulated contrasted silviculture scenarios, *i.e.* sequences of random thinnings where trees are progressively eliminated regardless of their phenotype before the reproduction phase, and different random mortality disturbance regimes, over four silvicultural cycles corresponding to four generations of trees. In these simulations, silviculture and disturbances are not directly selective and their only potential impact is to regulate competition and mating success. We assessed the relevance of the evolutionary rates on vigor predicted by the demo-genetic coupling with and without silviculture and disturbance in comparison to empirical estimates found in the literature. We compared the silviculture scenarios and disturbance regimes with regard to their impacts on the evolutionary rate and the forest productivity.

2. Materials and Methods

2.2. Purpose and general description of the model

Luberon2 simulates the evolution of demographic, dendrometric (various dimensions of trees) and genetic variables at forest scale, over multiple tree generations, under different scenarios defined by: (i) the genetic architecture of variable traits, (ii) the spatial environment, (iii) the initial population structure and genetic diversity, (iv) the disturbance regime and (v) the thinning regime.

Luberon2 results from the coupling of forest dynamics processes with disturbance regimes and quantitative genetic inheritance of traits (Figure 1). Each annual step in Luberon2 corresponds to an eco-evolutionary feedback loop where: (i) the genetic diversity determines the distribution of individual tree performances, *i.e.* growth, survival and reproduction; (ii) individual performances drive

the stand dynamics and structure; (iii) which in turn affect the intensity of the evolutionary drivers shaping the genetic diversity, i.e. genetic drift and selection. The distribution of individual tree performances is also driven by stochastic disturbances and silvicultural interventions, i.e. thinnings. Disturbances are modeled through their regimes of impacts, i.e. the frequency and intensity of occurrence of mortality events with a dynamic control by stand-level and tree-level characteristics. Luberon2 simulates within-generation dynamics and inter-generational evolution of monospecific even-aged stands, or irregular stands with even-aged substructure. Quantitative genetic variation is put on parameters of forest dynamics processes that ultimately drive individual tree survival and reproduction. Diverse thinning strategies can be simulated to regulate the stand dynamics. The model is developed on the Capsis modeling software platform (Dufour-Kowalski et al., 2012). Here, we provide a synthetic presentation of the model version calibrated for Atlas cedar, *Cedrus atlantica* (the model gets its name from an emblematic cedar forest in France, Luberon), but other species can be considered. Full description of the model is available online in a user manual (https://capsis.cirad.fr/capsis/help_en/luberon2).

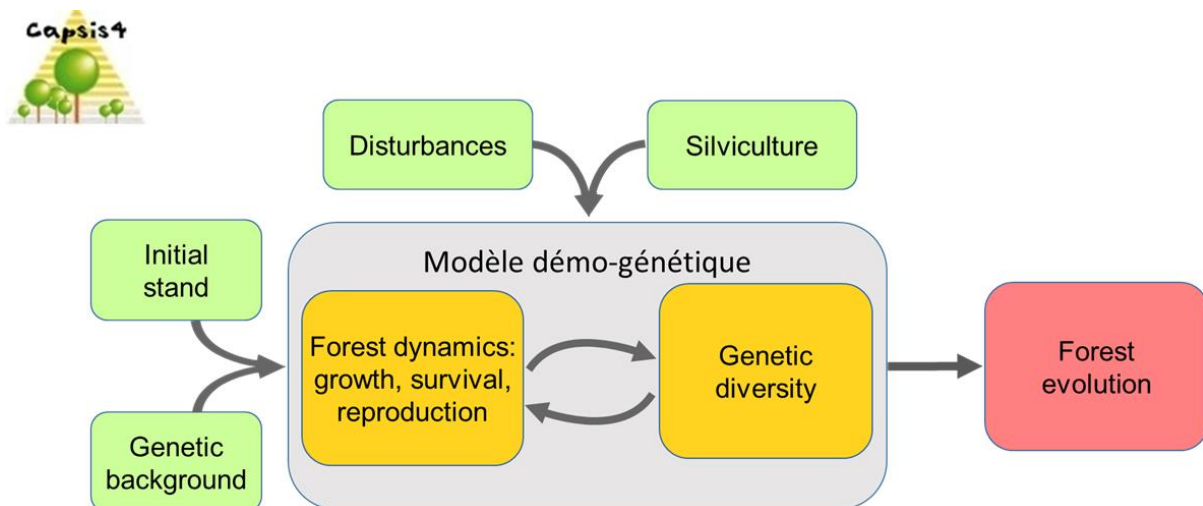


Figure 1. Main components of the Luberon2 demo-genetic agent based model, developed on the Capsis software platform: initial stand description and genetic background, disturbance regimes and silvicultural scenarios are the inputs (green boxes), demo-genetic processes (gray box) result from the coupling of a forest dynamics model with genetic diversity and inheritance model (orange boxes), stand- and tree-level dynamic variables regarding the demography, performances and genetic diversity are the outputs (red box)

Objects and their variables

The main object is a *scene*, which includes the lists of trees and geographic elements (Appendix 1). Each individual tree belongs to a *parcel*, which is an area of spatially homogeneous environment defined by a spatial polygon and an index of environmental quality, here measured by

the so-called site index, *i.e.* height of the tallest trees at a given age. The parcel is also a management unit. To allow for spatial heterogeneity in stand structure and to proceed with regeneration, the scene is split into a regular grid of square **pixels**: during the simulations, each pixel is modeled as an independent even-aged stand where growth, competition and survival processes occur with no impact of its neighbor pixels. The only interaction among pixels occurs during the regeneration phase through seed and pollen flow. Pixel size is configurable, 15m x 15m by default, with possible consequences on the prediction of stand-scale dendrometric variables (Appendix 2A).

Individual trees have fixed attributes like spatial coordinates, multi-locus genotype, parents' identity, consanguinity, as well as dynamic attributes that evolve during simulation like age, dendrometric and fecundity variables, phenotypic value (see the user manual for a detailed list of individual tree attributes). The initial individual trees are defined in the inventory input file, then new individual trees are created by the model during the regeneration process. In the initial inventory, if the individual tree diameters are not provided, they are drawn from the expected distribution of diameter given tree age and stand density.

Succession of processes in a simulation step

Simulations proceed at 1-year temporal resolution. Each year, the succession of processes is the following: growth, mortality through self-thinning, mortality through disturbance, regeneration; and silviculture interventions are applied at the end of the annual step (Appendix 1).

Growth model

In each pixel, the diameter growth of each individual tree is computed by correcting the baseline prediction of a distance-independent tree growth model, which accounts for competition, with an additive term representing the individual phenotypic value of vigor (as explained below in the genetic model). Here, the growth model is calibrated for Atlas cedar (Courbet, 2002) but the same type of growth model is widely applied for other species in pure even-aged stands (Dhôte, 1991; Deleuze et al., 2004). Briefly, this segmented growth model computes the stand-level annual increment in basal area, *i.e.* the cross-sectional area of trees at 1.3m above ground, then transformed in individual diameter increment, with null increment for trees below a threshold circumference value, and increment increasing linearly with tree circumference above this threshold (Appendix 3). The parameters of this empirical function vary dynamically according to dendrometric characteristics of the growth unit, such as density and dominant height (height of the tallest trees). Other dendrometric

variables at tree level and pixel level are then derived from the radial tree growth. The growth model was calibrated for trees above a certain age, namely the recruitment age (25 years for Atlas cedar).

Self-thinning mortality model

In each pixel, after annual tree growth, self-thinning occurs if the number of trees exceeds the maximum number of trees that depends on the root mean square of circumferences. The smallest trees are progressively eliminated one by one until reaching a relative density index value below the maximal density, following a relation calibrated for Atlas cedar (Courbet, 2002).

Regeneration model

Trees are considered fertile if they are older than the recruitment age and have a diameter above a threshold diameter value (15cm for Atlas cedar). The annual production of cones by a female tree is determined as an ordinal variable related to tree diameter and crown height with inter-annual (for each tree) and inter-individual (among equal-size trees) stochasticity: this relation and the mean number of viable seeds per cone were calibrated on Atlas cedar (Appendix 3). Individual male fertility is a relative value equal to the square of tree diameter.

In each pixel where regeneration occurs, at each year during the regeneration period, individual seedlings (not seeds) are established. By default, the number of seedlings established in a pixel is arbitrarily scaled to the predicted seed rain received in 1m^2 at the center of the pixel from all mother trees of the scene, which ends in the range of seedling density values observed in Atlas cedar regeneration plots (this can be changed by the user, see further discussion in Appendix 2B).

The composition of the seedling cohort in each pixel is determined by the contribution of all mother-trees given their female fecundity and their distance to the center of the pixel following a 2D-exponential dispersal kernel calibrated for Atlas cedar seeds (E. Klein pers. comm.). Once a seedling is established and its mother-tree assigned, its father-tree is determined among the fertile trees with a probability that depends on their male fertility and distance to the mother tree following a pollen dispersal kernel function. The genotype of each seedling is then derived from the genotypes of its parents, accounting for stochastic gamete sorting and recombination. Since this is a finite-loci model to simulate short to mean term evolutions, i.e. only a few generations of trees, mutations are neglected.

Each new seedling is initialized with a diameter drawn from the expected distribution of diameter at recruitment age given tree density, and it doesn't grow until reaching this age. When

recruitment starts, since the growth model is calibrated for even-aged cohorts, the adult trees that may eventually remain in the pixel are removed to let the recruited seedlings grow, self-thinning operates to regulate the density of recruited seedlings, and the age of all accumulated seedlings over the regeneration period is set to the recruitment age. Note that the initial diameter of a new seedling is drawn at random but its genotypic value for vigor is derived from the parents. Thus, the genotype only starts to influence tree diameter after the first step of growth. In other words, the inter-individual variation resulting from all kinds of pre-recruitment processes is considered to be neutral with regard to the quantitative traits in the model, and the genetic variation only acts on post-recruitment processes.

Mortality through random disturbance

In *Luberon2*, stochastic disturbances are simulated through their quantitative impacts on the demographic processes of growth, survival and/or reproduction. The disturbance regime of impacts is characterized by the distribution of impact intensities, their frequency of occurrence and, eventually, spatial patterns of impacts. The regime of impacts of a disturbance can be calibrated on empirical surveys independently of the level of knowledge on the biological mechanisms of response. Here, we considered stochastic disturbance killing trees randomly, regardless of their individual characteristics. Each year, the intensity of a stochastic hazard is drawn from a bimodal distribution combining frequent low values and rare high values (combined Weibull distributions where low values are five times more frequent than high values), representing the potential probability of death. This probability is first modified at pixel level by the sum of crown heights, i.e. the probability of death is locally reduced where trees are fewer and/or smaller: this type of density-dependent regulation occurs with abiotic stresses or biotic interactions. Additionally, the model allows further adjustment of the probability of death at individual level based on genetic sensitivity to this disturbance, an option that is not used in the following simulations.

Here, we considered two levels of random disturbance regimes (in addition to scenarios with no disturbance at all). A medium disturbance regime was obtained by drawing the annual intensity of the hazard in a unimodal Weibull distribution reaching an average annual mortality rate around 2%, which corresponds to observed rates in other species (Petit-Cailleux et al., 2021). A severe disturbance regime was obtained by drawing the annual intensity in a bimodal Weibull distribution of frequent low intensity events and rare high intensity events, reaching an average annual mortality rate around 12%.

Silvicultural interventions and scenarios

Luberon2 implements various types of silvicultural interventions (called “harvest” when all the trees are removed and “thinning” when only some trees are removed). Thinning criteria can be defined at stand level (*e.g.* target tree density or target basal area with thinning from below, *i.e.* removing smaller trees, or thinning from above, *i.e.* removing bigger trees, or random thinning, *i.e.* removing trees randomly) or at individual tree level (*e.g.* age, size or spatial criteria, or any combination of those). In this study, all interventions were selectively neutral, *i.e.* we applied random thinnings with no choice of the trees to cut.

The simulations were initialized with a 25-years old Atlas cedar forest, consisting of one environmentally homogeneous parcel of 4.41 ha with a density of 2800 trees/ha, and a site index of 20 m at 50 years. We applied seven silvicultural scenarios in four successive cycles repeating the same sequences of interventions with non-overlapping generation turnover (Appendix 1). The silvicultural scenarios differed in terms of cycle length (60 or 100 years), time and intensity of thinning interventions (Table 1). For all scenarios, each management cycle (including the fourth) ended with three years of regeneration triggered by an intervention called the seeding cut, leaving 110 seed trees/ha. At the end of these three years, the final harvest removed the seed trees to leave only the new seedlings. The number of created seedlings was determined by the regeneration model, but we reduced this number at the age of recruitment to reset the initial value of 2800 trees/ha (using random thinning) to avoid any effect of demographic stochasticity at the regeneration step blurring the impact of silviculture interventions. In two unthinned scenarios (named U-long and U-short for long or short cycle, respectively), we only applied the seeding cut and the final harvest to allow regeneration, control the cycle length and harmonize the number of seed-trees contributing to the regeneration with the other scenarios. As baseline scenarios for long and short cycle management (B-long and B-short), we followed silviculture guidelines for Atlas cedar in France (Ladier et al, 2012; and CNPF, 2020, respectively). To disentangle the effects of intensity and frequency of thinnings, we also derived three exploratory scenarios from the B-long scenario: in a low intensity scenario (E-low) we performed all thinnings with higher target tree density values than in the reference, in a delayed scenario (E-delayed) we skipped the thinnings at juvenile stage and kept the remaining thinnings with the same target density as in the reference, and in a relaxed scenario (E-relaxed) we skipped the late stage thinnings (Table 1).

Table 1. Sequences of thinnings in the different silvicultural scenarios: stand age at intervention and, in brackets, target tree density after the intervention. Each cycle ends with a seeding cut harmonizing the density of seed trees over all scenarios, and a final harvest of seed trees after three years of reproduction. In the four cases where thinning 1 is omitted, seedling density is nevertheless reduced at age 25 to the same value as initialization, *i.e.* 2800 trees/ha, for harmonization. All interventions are made randomly with no tree choice.

Scenario	thinning 1	thinning 2	thinning 3	thinning 4	thinning 5	thinning 6	seeding cut	final harvest
U-long: Unthinned, <i>long cycle</i>	-	-	-	-	-	-	100 (110)	103 (0)
U-short: Unthinned, <i>short cycle</i>	-	-	-	-	-	-	60 (110)	63 (0)
B-long: Baseline, <i>long cycle, thinning</i>	25 (1100)	40 (600)	50 (430)	60 (320)	70 (245)	80 (200)	100 (110)	103 (0)
B-short: Baseline, <i>short cycle, thinning</i>	25 (1100)	30 (600)	40 (200)	-	-	-	60 (110)	63 (0)
E-low: Exploratory, <i>long cycle, low intensity thinning</i>	-	40 (2400)	50 (1720)	60 (1280)	70 (980)	80 (800)	100 (110)	103 (0)
E-delayed: Exploratory, <i>long cycle, delayed thinning</i>	-	-	-	60 (320)	70 (245)	80 (200)	100 (110)	103 (0)
E-relaxed: Exploratory, <i>long cycle, relaxed thinning</i>	25 (1100)	-	-	-	70 (245)	80 (200)	100 (110)	103 (0)

Genetic model

Luberon2 uses a finite-loci quantitative genetic model to represent within-stand phenotypic variation. The management of genetic information, *i.e.* the effect of the genotype on the phenotype and sexual reproduction processes, is piloted through the Genetics library of Capsis (Seynave & Pichot, 2004). Nuclear diploid individual genotypes are defined along a genetic map, which contains multi-allelic neutral loci (not used here) and diallelic quantitative trait loci controlling growth vigor.

Each diallelic QTL is characterized by an absolute allelic effect, with a positive value for the allele increasing the value of the trait, and a negative value for the alternative counterpart decreasing the value of the trait. For each variable trait, the model assumes additive inheritance: the genotypic value of an individual is the sum of the effects of its alleles over the QTL controlling the trait and, therefore, a full heterozygous individual has a null genotypic value. At each simulation step (year), the individual phenotypic values are computed as the sum of the genotypic value with an individual environmental term made of two components: a fixed component and an “inter-step” component that randomly varies annually.

Here, we used an heuristic algorithm to produce the initial genotypic data with the following sets of target genetic parameters (more information on this algorithm in the Luberion2 user manual). Individual vigor, *i.e.* the individual deviation to the baseline prediction of individual diameter increment as previously defined, was the only variable trait. The response to selection depends on the initial genetic variance and, for a given initial variance, changes in genetic mean and variance depend on the genetic architecture of the trait, *i.e.* the number of QTL, the distribution of allelic effects, and the allele frequencies. To test the sensitivity of the model to assumptions made on the genetic architecture of the variable trait, which is generally unknown, we fixed the initial additive variance of vigor and considered two cases of genetic architecture, either 10 or 50 QTL, which are expected to result in slightly different micro-evolutionary outcomes (Cubry et al, 2022). We considered two cases of initial population: a reference with no phenotypic variation of vigor, *i.e.* no QTL effects and no environmental variance, and a panmictic population with genetic and environmental variation. In the second case, we fixed the additive genetic variance at $VA = 0.0042$ with a null “inter-step” component of the environmental variance, which corresponds to the average within-population variance estimated in 22 populations of five tree species (Fririon et al, 2023), and the narrow sense heritability at $h^2=0.3$, which is usually found for growth related traits (Cornelius, 1994; Alberto et al, 2013). It is worth noting that even in the case without phenotypic variation of vigor there is a background inter-individual variation of tree size driven by the growth process, depending on the initial tree sizes and local growth and competition processes.

To reach the target genetic variance, the algorithm optimizes both the distribution of allelic effects, following an L-shape distribution with few QTL of large allelic effect, and the distribution of allelic frequencies. Therefore, running the algorithm several times with the same target values results in different sets of allelic effects, allelic frequencies and genotype frequencies. In the following simulations, we assessed the sensitivity of the model to this genetic initialization stochasticity by running five optimizations for each set of target genetic parameters for the scenario with non-null genetic variance of vigor.

Finally, we used 11 initial genetic backgrounds: one reference case without phenotypic variation and ten cases with the same additive variance, either with 10 or 50 QTL, five different genetic setups of allelic effects and frequencies in each case, with linkage equilibrium at the start.

How selection proceeds in the demo-genetic model

Selection proceeds through differential survival (viability selection) and contribution to the regeneration (male and female fecundity selection). Natural mortality by competition, *i.e.* self-

thinning, is selective with regard to tree size. In this context, tree size is a key fitness component because it is the direct target of viability and fecundity selective processes. Therefore, indirect selection on vigor dynamically emerges from the model because vigor is a variable trait contributing to tree size through the growth model. The intensity of indirect selection on vigor depends on its correlation with tree size, which dynamically varies with age, competition and disturbances. More generally, in DG-ABMs, selection intensity is not a fixed parameter, it varies dynamically with the stand structure, the disturbance regime, and silvicultural interventions.

By contrast, in the following simulations, mortality by disturbance and by silviculture were not selective because there was no variation for sensitivity to disturbance and thinnings were random. Here, the only consequence of random disturbance and random silviculture was to reduce the population density, hence reducing the intensity of indirect natural selection on vigor by competition.

2.2. Simulation plan and analysis of simulation outputs

The full factorial design combining 11 genetic backgrounds with seven silvicultural scenarios and three disturbance regimes resulted in 231 scenarios that were replicated 10 times to account for stochasticity in the regeneration compartment of the model, i.e. leading to 2310 simulation runs in total.

For each simulation run, i.e. four successive cycles of the same silvicultural regime, the dendrometric and genetic variables were stored annually (Table 2). Annual changes within a cycle informed on the mechanisms that progressively generate the selection differential between the subset of reproductive trees and the original population, while inter-generational changes also accounted for the effect of mating success and heredity processes. We computed the average evolutionary rate per generation for vigor over the whole period of time, H_0 , defined by Gingerich (1993; 2009) as:

$$H_0 = (zdiff_i / \sqrt{zvar.w_i}) / n.gen \quad (equation 1),$$

where $zdiff_i$ is the observed change in the mean value of the trait in a temporal interval i , $zvar.w_i$ is the pooled within-population phenotypic variance of the trait sampled at the beginning and at the end of the temporal interval i , and $n.gen$ is the number of generations. The temporal interval i that we used is defined by the beginning of the first silvicultural cycle and the regeneration produced after the fourth, corresponding to four complete generations.

Here, there is a typical eco-evolutionary feedback: selective competition on tree size generates an indirect selection on vigor, and the genetic gain on vigor may increase tree size and thus

increase selective competition intensity. To study these feedback effects of genetic evolution on predicted forest productivity, we used two stand-level variables classically used in forestry, the dominant diameter (diameter of the tallest trees, *Ddom*) and the basal area production (here accumulated through time, *BAprod*), as integrative variables jointly driven by the population genetic mean of vigor, the population heterogeneity, and the intensity of competition.

Table 2. Description of the Luberon2 output variables analyzed in this study.

Output variable	Code	Unit	Description
<i>Number of trees per hectare</i>	<i>Nha</i>	-	The number of alive individual trees per hectare.
<i>Population genetic mean of vigor</i>	$\mu G.Vig$	cm.year ⁻¹	The population genetic mean of vigor. The initial mean is 0, then evolutionary processes, e.g. genetic selection and drift, cause the value to evolve.
<i>Additive genetic variance of vigor</i>	<i>VA(Vig)</i>	cm ² .year ⁻²	The variance of individual vigor genetic values within the population.
<i>Heterozygosity</i>	<i>He</i>	-	Nei's expected heterozygosity
<i>Dominant diameter</i>	<i>Ddom</i>	cm	The mean diameter of the 100 tallest trees per hectare.
<i>Basal area production</i>	<i>BAprod</i>	m ² /ha	Sum of cross-sectional areas measured at 1.3 m of all cut trees from the first thinning to the final harvest.
<i>self-thinning-induced deaths</i>	<i>DeadS-T</i>	-	Number of deaths per hectare by self-thinning in a single silvicultural cycle.
<i>disturbance-induced deaths</i>	<i>DeadD</i>	-	Number of deaths by disturbance per hectare in a single silvicultural cycle.

3. Results

3.1. Natural selection on vigor through differential mortality and reproduction in the unthinned scenario without disturbance

We first characterized the process of natural selection on vigor that emerged from the model in the unthinned long cycle scenario (U-long) without disturbance, with phenotypic variation of vigor. Over four consecutive cycles, the genetic mean continuously increased, both within- and across generations, while the evolution of the genetic variance resulted from the alternance of erosion

(within-generation) and restoration (at reproduction) phases (Figure 2). Within each generation, once self-thinning started, viability selection proceeded continuously with annual changes of the genetic mean and variance of vigor, with a progressive decrease in the rate of change of the mean. This progressive decrease resulted from the combined effects of three mechanisms: (i) the erosion of standing variance available for selection, which progressively reduced the response to selection; (ii) the decrease of mortality rate by self-thinning while population density decreased (Figure 3ab), which progressively reduced selection intensity; and (iii) the progressive increase of the correlation between vigor and tree size during stand development (data not shown), which increased the strength of indirect selection on vigor. At each regeneration step, sexual reproduction restored the genetic variance and generated a high density of young trees, thus restoring the dynamics of selective competition. In these simulations, fecundity selection only occurred during the three years of reproduction at the end of each cycle.

The evolutionary trends were similar with 10 QTL and 50 QTL, but the variation between genetic setups was higher with 10 QTL (Figure 2). On average, the increase of the genetic mean was lower with 10 QTL than with 50 QTL with some heterogeneity among setups, but the erosion of the genetic variance and QTL gene diversity (H_e) was systematically more pronounced with 10 QTL than with 50 QTL. The variation among ten replicates with the same initial genetic setup, resulting from stochasticity in the reproduction process, was negligible except for the predicted changes in genetic variance with 50 QTL and, in this case, it remained much less than the variation due to genetic architecture assumptions (Figure 2).

In the next sections, we focus on one setup of the 50 QTL case: the results obtained with all genetic backgrounds were consistent with this particular case and are provided in Appendix 4.

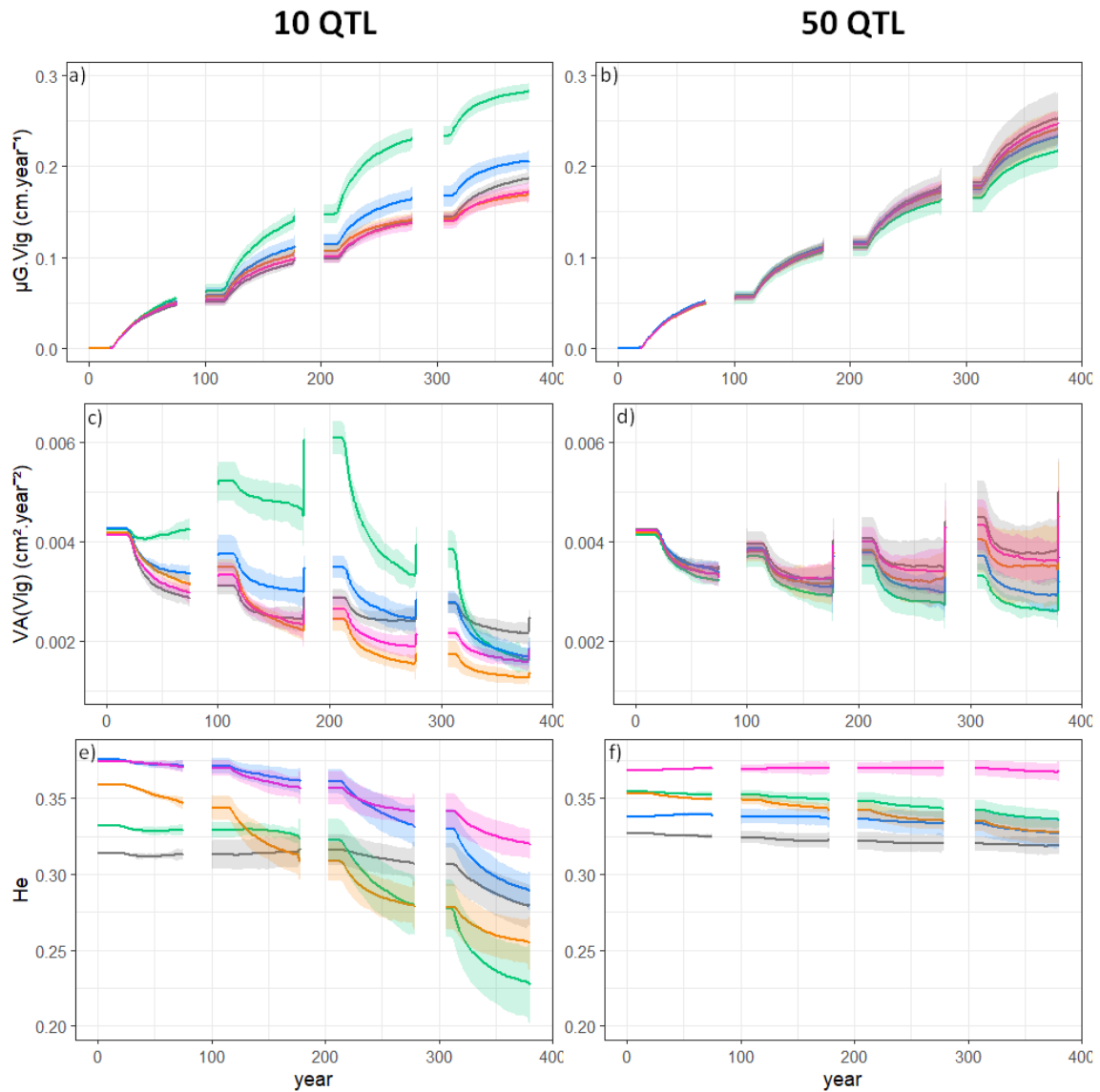


Figure 2. Dynamics of population genetic parameters in the unthinned long cycle scenario (U-long) without disturbance for 10 QTL and 50 QTL (in columns): population genetic mean, $\mu G.Vig$ (a, b); genetic variance, $VA(Vig)$ (b, c); and QTL gene diversity, He (e, f). The different colors indicate five genetic setups, *i.e.* combinations of allelic effects and allelic frequencies representing the same target additive genetic variance. The shaded areas represent the 95% intervals over 10 replicates for each genetic setup. Trees are 25-years old when simulations start at year 0. The pre-recruitment period is deliberately not represented because the phenotype is not considered in the model during this phase.

3.2. Feedback effect of selection on population dynamics in the unthinned scenario without disturbance

We explored the feedback effect of genetic evolution on the demographic dynamics in the unthinned long cycle scenario (U-long) without disturbance by comparing the simulations with vs. without phenotypic variation of vigor. Without phenotypic variation of vigor, the dynamics of

mortality by competition remained stable across generations: once the stand reached the density to initiate self-thinning (here at age 43), mortality rapidly increased to a maximum rate and then progressively slowed down while density decreased (Figure 3ab). With phenotypic variation, the progressive selection of more vigorous individuals within each cycle resulted in higher mortality rate by competition and, therefore, the stand density was lower than without phenotypic variation (Figure 3b). Furthermore, the genetic improvement of vigor was associated with an increase in self-thinning mortality rates across generations (Figure 3a).

Without phenotypic variation of vigor, the growth model predicted a dominant diameter of 40 cm at the end of each silvicultural cycle (Figure 3c), and the cumulated basal area production over four cycles reached 616 m².ha⁻¹ (Figure 3d). The presence of phenotypic variation of vigor progressively increased the variance of tree diameter within each silvicultural cycle, and the selective elimination of less vigorous individuals before reproduction led to a progressive increase in stand productivity across generations, *i.e.* a genetic improvement process: the average genetic gain on dominant tree diameter was 11% per generation, and the cumulated basal area production over four cycles reached 1127 m².ha⁻¹.

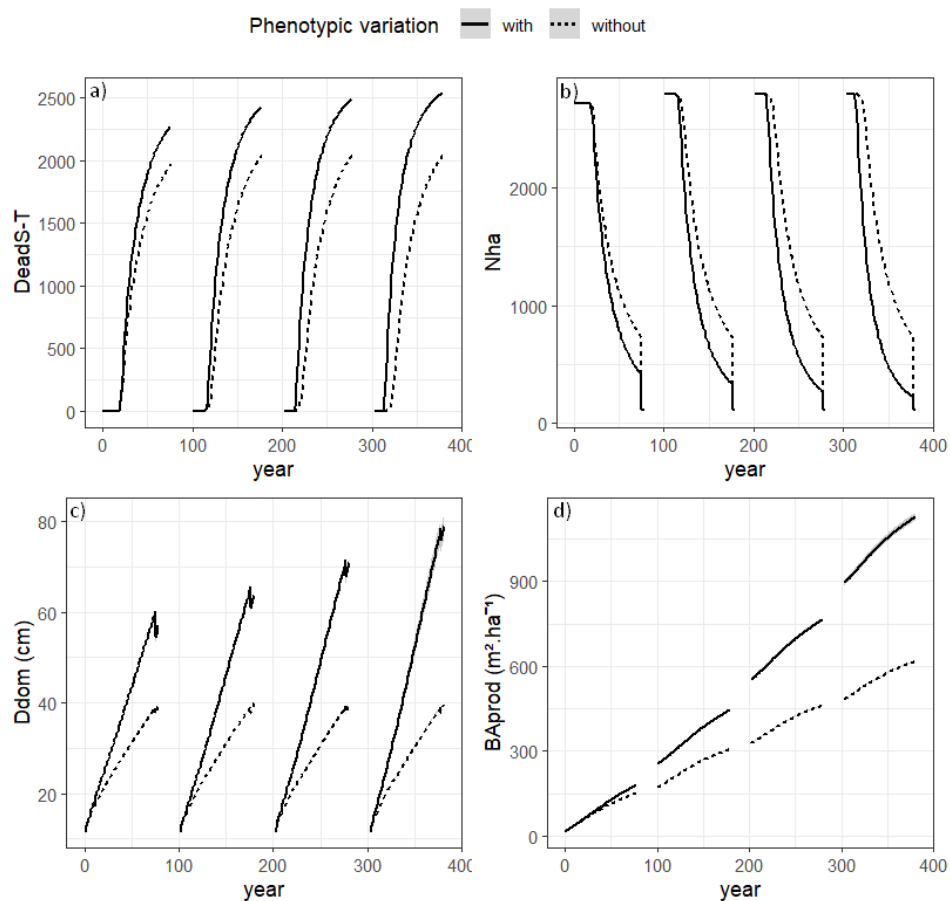


Figure 3. Dynamics of dendrometric and demographic variables in the unthinned long cycle scenario (U-long) without disturbance, with or without phenotypic variation (line types): a) number of deaths by self-thinning per hectare, $DeadS-T$; b) number of trees per hectare, Nha ; c) dominant diameter, $Ddom$; d) cumulated basal area production per hectare, $BAprd$. This figure illustrates one genetic setup with 50 QTL, see Appendix 4 for the other genetic setups. The 95% intervals over 10 replicates, represented by shaded areas, are imperceptible. Trees are 25-years old when simulations start at year 0. The pre-recruitment period is deliberately not represented because the phenotype is not considered in the model during this phase. (Note: in c), the small drops in dominant diameter at the end of each cycle correspond to the seeding cuts: this random intervention is likely to remove the largest trees by chance).

3.3. Impacts of thinning scenarios and disturbance regimes on natural selection and evolutionary rates

We compared simulations implementing different silvicultural scenarios (Table 1) and disturbance regimes (null, medium, high), including always phenotypic variation of vigor, to investigate their joint impacts on the natural selection process and overall evolutionary rates. In the unthinned long cycle scenario (U-long) without disturbance, selective self-thinning was the only mechanism of mortality (Figure 4a) and viability selection by competition was the main driver of genetic evolution in vigor, with negligible additional effect of fecundity selection (Figure 4c). In the baseline long cycle scenario with thinning (B-long), the non-selective decrease of tree density reduced the rate of mortality by self-thinning (Figure 4a), thus reducing the intensity of viability selection to a negligible level, and the only mechanism of selection was fecundity selection causing qualitative leaps in mean vigor at the time of reproduction (Figure 4c). Similarly, disturbance acted as another form of non-selective mortality reducing population density and competition intensity (Figure 4b). With the medium disturbance regime, self-thinning persisted in the unthinned long cycle scenario but it was reduced by 73% on average and, consequently, the selection differential on vigor, *i.e.* the difference between the genetic mean of seed trees and that of the initial population at the beginning of the cycle, was reduced by 63% on average. In the baseline long cycle scenario with thinning with medium disturbance regime, viability selection by self-thinning did not occur anymore (Figure 4). The severe disturbance regime caused a population collapse at the end of the first generation.

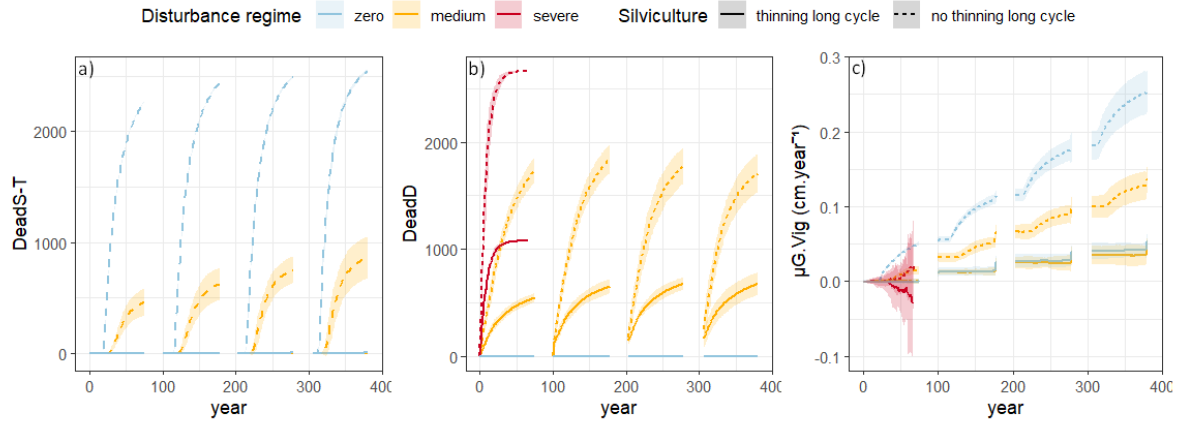


Figure 4. Dynamics of mortality and genetic changes in the long cycle scenarios with phenotypic variation, with or without thinnings (B-long or U-long, respectively, line types) and three disturbance regimes (colors): a) deaths by self-thinning, *DeadS-T*; b) deaths by disturbance, *DeadD*; c) population genetic mean of vigor, $\mu G.Vig$. This figure illustrates one genetic setup with 50 QTL, see Appendix 4 for the other genetic setups. The shaded areas represent the 95% intervals over 10 replicates for each scenario. With the severe disturbance regime, the population collapsed during the first cycle. Trees are 25-years old when simulations start at year 0. The pre-recruitment period is deliberately not represented because the phenotype is not considered in the model during this phase.

Comparing unthinned scenarios with long or short cycle (U-long and U-short, respectively), viability selection by competition was the main evolutionary force increasing population genetic mean in both cases, the short cycle induced shorter exposure to selective competition but concentrated on early stages when competition was maximum, and also more opportunities for fecundity selection, finally resulting in a slightly lower genetic mean at most dates (Figure 5). By contrast, in the baseline scenarios with thinning (B-long and B-short), random thinnings impeded viability selection by competition, and fecundity selection remained the only driver of changes in population genetic mean (Figure 5). In this case, the short cycle scenario having more frequent reproductive events than long cycle scenarios also reached higher genetic mean at a given date (Figure 5), despite lower evolutionary rate per generation (see below). Thus, the impact of the length of silvicultural cycles depended on the importance of viability selection by competition, *i.e.* on the relative role of self-thinning and random thinning by management.

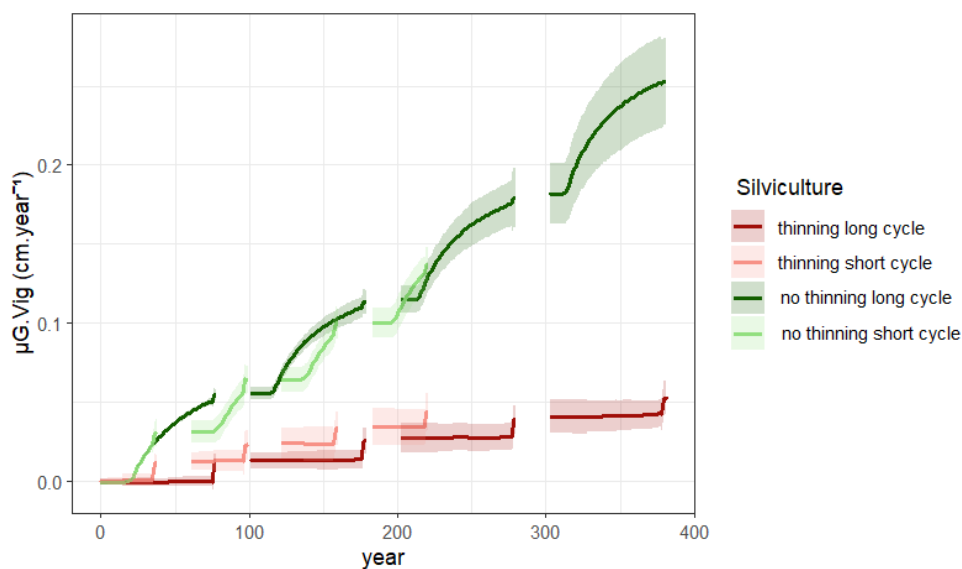


Figure 5. Dynamics of the population genetic mean of vigor ($\mu G.Vig$) in four scenarios, long or short cycle with or without thinnings (B-long, B-short, U-long, U-short, respectively, in colors). This figure illustrates one genetic setup with 50 QTL, see Appendix 4 for the other genetic setups. The shaded areas represent the 95% intervals over 10 replicates for each scenario. Trees are 25-years old when simulations start at year 0. The pre-recruitment period is deliberately not represented because the phenotype is not considered in the model during this phase.

The more intensive the random thinning (from unthinned to exploratory and baseline thinning scenarios, from long to short cycle) or disturbance regimes, the higher reduction in selective competition and the lower the evolutionary rates (Figure 6). The unthinned long cycle scenarios (U-long) resulted in the highest evolutionary rates of vigor for each disturbance regime, ranging from 0.35 to 0.62 when there was no disturbance depending on the number of QTL and the genetic setup (Appendix 4). In comparison, the exploratory low intensity thinning scenarios (E-low) reduced the evolutionary rate by 9% on average over the disturbance regimes, and other scenarios resulted in higher reduction, in the following order: exploratory delayed thinning scenarios (E-delayed, by 45%), unthinned short cycle scenarios (U-short, by 47%), exploratory relaxed thinning scenarios (E-relaxed, by 59%), baseline long cycle scenarios (B-long, by 80%), and finally baseline short cycle scenarios (B-short, by 84%). On average over all silvicultural regimes, the medium disturbance regime reduced the evolutionary rates by 46%. The severe disturbance regime caused a population collapse that did not allow genetic evolution.

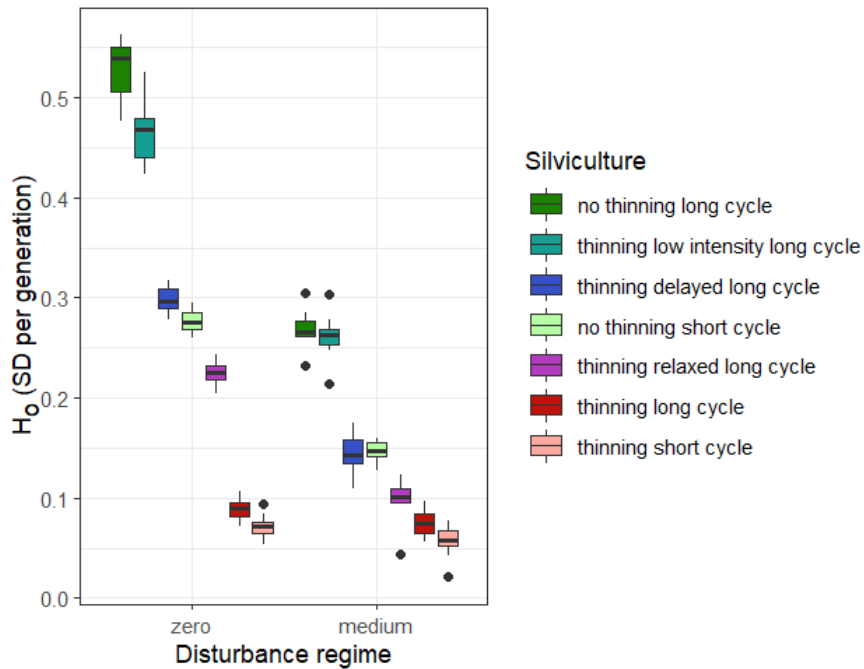


Figure 6. Average evolutionary rate (H_0) in vigor after four generations for the different silvicultural scenarios (following Table 1, in colors) and disturbance regimes (x-axis, the severe disturbance regime is not represented because it led to population collapse). The boxplots illustrate the distribution of values over 10 replicates in each case. This figure illustrates one genetic setup with 50 QTL, see Appendix 4 for the other genetic setups.

3.4. Impacts of thinning scenarios and disturbance regimes on forest productivity

Finally, we compared simulations implementing different silvicultural scenarios, different disturbance regimes, and including or not phenotypic variation of vigor, to highlight the interaction between silviculture, disturbance and genetic evolution on forest productivity. The impact of the thinning regime on the cumulated basal area production over four cycles was highly dependent on the phenotypic variation and disturbance regime (Figure 7). Without phenotypic variation and without disturbances, more frequent and intensive random thinnings increased the basal area production. This could be explained because random thinnings relaxed the competition with a direct positive effect on individual tree growth. With phenotypic variation and no disturbance, the pattern was exactly the opposite: more frequent and intensive random thinnings resulted in lower basal area production. Furthermore, the basal area production obtained without thinnings was much higher in the case with phenotypic variation than without, due to the feedback effect of selection on population dynamics mentioned above (see section 3.2). Thus, with phenotypic variation, competition had a positive selection effect on the mean vigor that counterbalanced its negative effect on individual tree growth. In these simulations, the effects of thinning regimes on the basal area production were directly

correlated with their impact on the evolutionary rate of vigor as previously shown (Figure 6), *i.e.* less frequent and less intense random thinnings increased the evolutionary rate and the cumulated basal area production. With the medium disturbance regime, random disturbances reduced the intensity of selection by competition, thus reducing the difference in selection intensity between the unthinned or low intensity thinning scenarios and the others. Consequently, with phenotypic variation and disturbances together, the difference of cumulated basal area production among thinning regimes was very low (Figure 7).

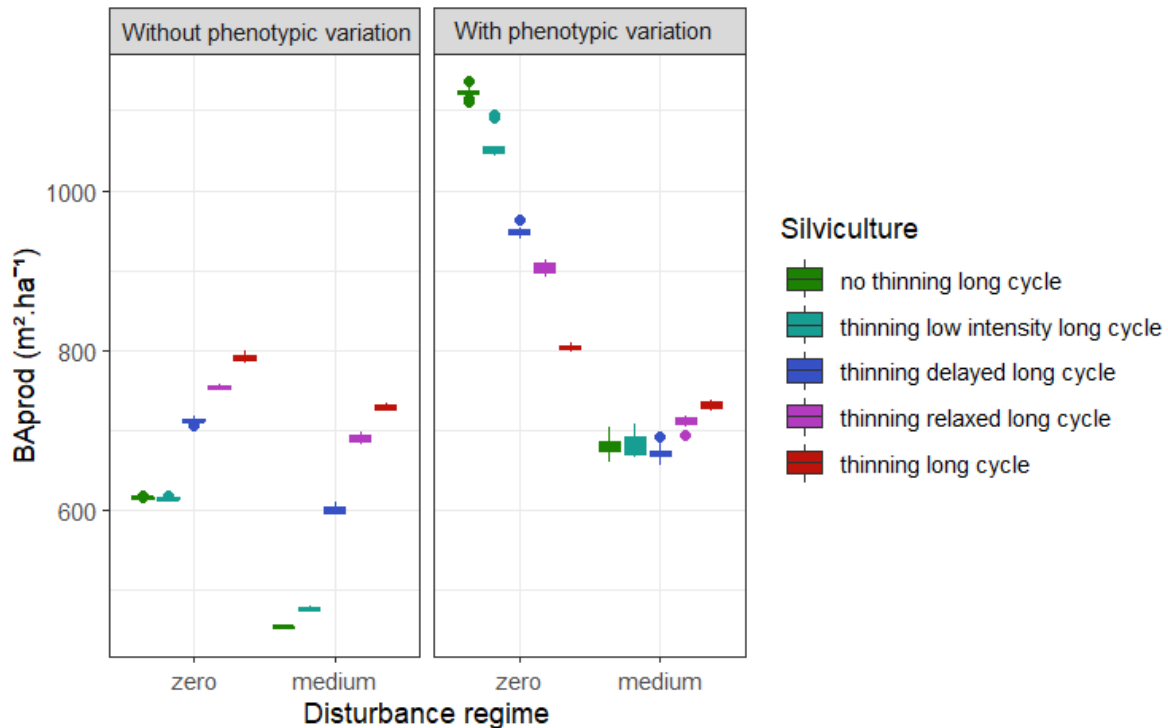


Figure 7. Basal area production (BA_{prod}) at the end of the fourth silvicultural cycle in the unthinned (U-long), baseline thinning (B-long), exploratory low intensity thinning (E-low), exploratory delayed thinning (E-delayed) and exploratory relaxed thinning (E-relaxed) long cycle scenarios (colors), depending on the level of phenotypic variation (panels) and disturbance regimes (x-axes, the severe disturbance regime is not represented because it led to population collapse). The boxplots illustrate the distribution of values over 10 replicates in each case. This figure illustrates one genetic setup with 50 QTL, see Appendix 4 for the other genetic setups.

4. Discussion

4.1. Range of predicted evolutionary rates and sensitivity to genetic assumptions

This study highlights the power of the demo-genetic modeling approach to investigate the interference between evolutionary and demographic processes, *i.e.* how population dynamics

predictions are affected by evolutionary processes and, vice-versa, how evolutionary rate predictions are affected by demographic processes. Here, we developed a demo-genetic forest model, Luberon2 by integrating genetic variation of a trait central to the demographic processes, vigor, which directly drives growth, survival and fecundity, in an individual-based forest growth model. This represents a situation of particularly strong interference between evolutionary and demographic processes. The comparison of contrasted simulation scenarios allowed us to disentangle the short-term and long-term impacts of demo-genetic coupling on the prediction of population dynamics, within- and across-generations respectively. The short-term impacts only depend on the amount of stable inter-individual variation, whether it be genetically or environmentally controlled, whereas the long-term impacts also depend on the heritability and genetic architecture. In our simulations over four generations, the evolutionary process increased the predicted dominant tree diameter by 11% per generation. We expect a lower impact of evolutionary processes on population dynamics when the variable traits are less tightly connected to the demographic processes. If we now look in the other direction, *i.e.* the impact of population dynamics on evolution, the predicted evolutionary rates on vigor were maximum in the absence of random thinnings and disturbances. In these conditions, considering a plausible level of initial additive variance and several genetic architectures, the predicted evolutionary rates were in the range of published empirical estimates for plant and animal populations: from 0 to 0.75 (Bone & Farres, 2001) and 0.1 to 0.3 (Gingerich, 2009), respectively. Therefore, we consider that Luberon2 can reasonably be used to characterize and quantify the eco-evolutionary feedbacks that emerge from demo-genetic coupling in the time frame of a few generations, as we did in this study. However, elaborating longer term predictions would require to account for the consequences of interference between evolutionary and demographic processes (*e.g.* by adding constraints on the long-term response to selection in the model).

The achieved evolutionary rate does not only depend on the standing variation and heritability, but also on the genetic architecture of the trait. Here, we investigated the sensitivity of the model to the number of QTL and to the distribution of allelic effects among QTL. The evolutionary rate was higher, and the erosion of additive variance and QTL diversity was lower, with 50 QTL than with 10 QTL. This difference may be attributable to the higher contribution of the covariance between QTL to the response to selection with 50 QTL than with 10 QTL (Cubry et al, 2022). However, the evolutionary predictions of the model were much less sensitive to the distribution of allelic effects and allelic frequencies with 50 QTL than with 10 QTL. Furthermore, our results suggest that the comparison among silviculture and disturbance scenarios is qualitatively robust to the assumptions on the genetic architecture of the trait of interest. In any case, since the genetic architecture of traits is rarely known

in detail, simulation studies based on DG-ABM may account for the sensitivity of the model to genetic architecture assumptions by including several genetic makeup scenarios in the simulation plan.

4.2. Mechanisms and intensity of natural selection on vigor in Luberon2

In forests, dominant trees have a competitive and reproductive advantage, which results in indirect selection on all genetically variable traits influencing tree size. Reproducing this mechanism in Luberon2, the selection gradient on vigor mechanically builds upon the integration of the phenotypic value in the growth function and upon the dynamic link between growth, mortality and reproduction processes. In this model, there is no selection on vigor during the juvenile phase before recruitment age because the initial diameter is randomly distributed among trees regardless of their genotypes at this age, selection on vigor may only start potentially once a correlation between vigor and diameter is established, *i.e.* after the first growth step, and it is effective once self-thinning starts. Annual changes in population genetic mean and variance within each generation inform on the mechanisms through which selection operates. In the baseline scenarios without thinning and without disturbance several mechanisms occur concurrently within each cycle: (i) self-thinning mortality started at age 43 and progressively decreased with age, which decreases the selection intensity; (ii) the genetic variance of vigor progressively decreases with age due to selective mortality, which decreases the response to selection; (ii) the correlation between vigor and tree diameter progressively increases with age while the contribution of the initial diameter at recruitment age decreases, which increases the selection gradient on vigor. In these scenarios, the third mechanism did not compensate for the other two, and the higher rate of change in the genetic mean and variance was observed at a very early stage, one or two years after the start of self-thinning mortality.

However, in reality, other patterns or processes not included in the model might reduce the intensity of selection on vigor. For instance, an environmental constraint to the phenotypic expression of vigor, a within-stand heterogeneity of disturbance regime, or a phenotypic trade-off between vigor and sensitivity to stress (Fririon et al., 2023), would reduce the correlation between vigor and tree size, thus reducing the intensity of indirect selection on vigor. A resource allocation trade-off between growth and reproductive functions (Wardlaw, 1990), or a life history trade-off between growth and longevity (Roskilly et al., 2019), would reduce the synergy of viability selection and fecundity selection on vigor. The ultimate consequences of such patterns and processes on the correlation between vigor and fitness, *i.e.* the selection gradient, are hardly predictable because this selection gradient dynamically results from complex interactions between multiple processes. Therefore, we consider that the evolutionary rates obtained in this study represent an upper bound, but still plausible, intensity of selection on vigor.

This study highlights the need to compare genetic mean and variances between generations at similar lifestage, as the annual fluctuations in genetic mean and variances within each generation may not faithfully represent the effective evolutionary signal passed from one generation to the next. For the trait of interest here, vigor, viability selection and fecundity selection mechanisms operated in the same direction, with a proportionally higher impact of the former in our conditions, resulting in a positive correlation between within-generation changes and inter-generational evolution. The situation was radically different for the genetic variance because each reproduction event compensated for the regular erosion that occurred during the viability selection process within the previous generation, resulting in weak inter-generational evolution of the variance despite intensive selection and erosion of the variance within each cycle. The restoration of the variance at reproduction was more efficient with 50 QTL than with 10 QTL, which relates to the higher role of covariance among QTL with 50 than with 10 QTL as previously mentioned. The restoration of the variance at each generation might be one of the reasons why standing variation is not a powerful indicator of the response to selection in wild populations (Pujol et al., 2018). For long-lived species like trees, this also underlines the risk taken in synchronic empirical studies that compare different life stages at a time (e.g. adults vs juveniles) to infer on genetic evolution: indicators of evolutionary changes should be measured at equivalent stages across different generations (Hansen et al., 2012), which may be challenging for long-lived organisms like trees.

4.3. Impact of neutral disturbance and management on natural selection

A major result of this study is that non-selective demographic events can have major indirect evolutionary consequences through their impact on natural selection processes. In these simulations, disturbance and thinning were neutral with regard to the trait of interest, vigor, as the mortality induced by these operations were vigor-independent. However, by reducing competition intensity, they reduced the intensity of natural viability selection due to self-thinning without directly affecting the intensity of fecundity selection, except that relaxing viability selection slightly increased the standing variance when fecundity selection occurs. Thus, compared to the baseline free evolution scenario, the evolutionary rates were reduced by disturbance alone, depending on the disturbance regime, and reduced by management alone, depending on the silviculture scenario. When both disturbance and management were combined, there was no synergy but rather an interaction effect so that the impact of disturbance on the evolutionary rate was reduced in the scenarios with management, and vice-versa. However, in reality, the negative impact of random thinning on the intensity of natural selection for vigor can be reinforced or balanced by the forester's tree choice, *i.e.* when non-random thinning is applied, either 'from below' or 'from above', at each step. Therefore, the evolutionary impact of real forest management combines both effects: the regulation of natural

evolutionary processes combined with direct or indirect anthropogenic selection, which can ultimately result in higher evolutionary rates of human-impacted contexts than in wild populations as observed in animal populations (Hendry et al, 2008). Various types of tree choice can easily be simulated with *Luberon2*, but addressing this management-induced selection requires an appropriate design to overpass contingency. Similarly, the negative impact of random disturbance may be reinforced or balanced in the case of size-dependent disturbance.

Our results show that shortening the silvicultural cycle has multiple impacts on natural selection. First, it increases the frequency of fecundity selection opportunities, with evolutionary consequences that depend on the correlation between vigor and fecundity at an earlier stage. Second, it shortens the exposure period to competition, with impacts on viability selection that depend on the competition intensity over the remaining exposure period, but it concentrates competition on the early stage when it may have high evolutionary impact. In our simulations, shortening the silvicultural cycle globally reduced viability selection and the associated genetic gain because self-thinning started late at age 43 and because vigor had no effect on competing ability before the recruitment age 25. However, in reality, the evolutionary consequences of shortening the silvicultural cycle would be very sensitive to the intragenerational demographic dynamics, which is complex and multifactorial, depending on the initial tree density, the local site fertility, the population vigor, the thinning and disturbance regimes.

These simulations illustrate how the coupled demo-genetic models can shed light on the mechanisms of eco-evolutionary feedback in a dynamic approach of the evolutionary forces. Here, considering a simple reference situation where competition for growth and reproduction are the only evolutionary drivers with non-selective management and disturbances, we understand the mechanisms through which competition intensity is both a selection pressure driving evolution and a consequence of the evolution of population mean vigor. In the context of global change that maintains populations out of equilibrium, such a dynamic approach of evolutionary forces is helpful to explore the potential impact of management and disturbance scenarios on the trajectory of genetic diversity and seek for multi-criteria management options.

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Appendices

Appendix 1 - Spatial and temporal scales in Luberon2

Appendix 2 - Consequences of the choice of pixel size

- A. consequences on stand growth and demography
- B. consequences on the regeneration process

Appendix 3 - Growth and fecundity functions

Appendix 4 - Supplementary Figures

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3. Ajouter du sélectif aux perturbations et aux interventions sylvicoles

3.1. Les perturbations, des moteurs de la sélection

Précédemment, nous avons considéré les perturbations comme des événements qui réduisent la population de façon non sélective, c'est-à-dire neutre vis-à-vis du génotype. Cependant, il s'agit ici d'une vision incomplète, et dans de nombreux cas les perturbations sont elles-mêmes moteur de la sélection. Par exemple, les traits de réponse au stress hydrique sont sous contrôle génétique et peuvent induire une réponse sélective importante dans des milieux où les sécheresses estivales reviennent chaque année (avec une intensité variable) (Liepe 2014 ; Bansal et al., 2015 ; Depardieu et al., 2020). Dans la suite de mes travaux, nous nous placerons dans le cadre de perturbations motrices de la sélection. Concrètement, nous considérerons non seulement les impacts directs des perturbations mais également la variation interindividuelle de ces impacts et l'héritabilité des traits associés.

3.2. Éclaircir par le bas pour suivre la direction du gradient de sélection

Comme pour les perturbations, nous avons considéré les interventions sylvicoles comme étant neutre vis-à-vis du génotype en simulant uniquement des éclaircies systématiques. En réalité, les forestiers utilisent de multiples critères pour choisir les arbres à abattre ou à favoriser. En plus des éclaircies systématiques, le sylviculteur a l'option de couper par le bas (supprimer les petits arbres), par le haut (supprimer les arbres dominants) ou encore d'effectuer des coupes sanitaires visant à retirer les arbres en mauvais état. Selon l'objectif, le jugement personnel du forestier et l'état du peuplement, les options d'éclaircies peuvent varier considérablement. Néanmoins, en particulier dans la conduite des futaies régulières, la première éclaircie est souvent systématique et les éclaircies suivantes visent à favoriser les arbres dominants (Perin et al., 2016), c'est-à-dire indirectement les génotypes à haut potentiel de croissance *a priori*. La sélection directionnelle sur la taille des arbres par la sylviculture est donc souvent alignée sur le gradient de sélection naturel déterminé par l'auto-éclaircie. La sélection par le sylviculteur pourrait en théorie aller plus loin que la sélection naturelle à condition que les interventions dépassent la mortalité qu'aurait produit l'auto-éclaircie seule et qu'elles sélectionnent efficacement les génotypes à forte croissance. Dans

la suite de mes travaux, nous nous placerons dans un cadre plus réaliste du point de vue du sylviculteur, en particulier en effectuant les éclaircies par le bas lorsque les itinéraires sylvicoles le prévoient.

VI - Conceptualiser et formaliser un régime d'impact de type sécheresse pour l'intégration dans un modèle DG-ABM

1. Les sécheresses : de l'aléa jusqu'aux impacts démographiques

Dans le contexte du changement climatique, on s'attend à ce que l'altération des régimes de sécheresses cause des changements particulièrement marqués des processus physiologiques, démographiques et évolutifs des peuplements forestiers. Certains auteurs suggèrent que l'impact direct le plus important du changement climatique sera lié au stress hydrique (par exemple, Allen & Breshears 1998). En effet, la disponibilité en eau peut expliquer jusqu'à 80% de la variabilité de croissance annuelle (Bréda et al., 2006), les sécheresses peuvent provoquer des épisodes de déclin des arbres à grande échelle dans les forêts tempérées (Allen et al., 2010), et les sécheresses montrent un fort potentiel synergique avec d'autres perturbations (ravageurs, incendies, etc.) (Seidl et al., 2017). En outre, les variations interindividuelles de réponse aux stress hydriques peuvent être importantes au sein des populations et induire une réponse sélective (Liepe 2014 ; Bansal et al., 2015 ; Depardieu et al., 2020). Dans ce contexte, J'ai fait le choix de recentrer mon travail sur l'aléa sécheresse.

1.1. De la physiologie...

Les conséquences physiologiques d'une sécheresse sont multiples pour l'arbre. La contrainte croissante due aux épisodes de déficit hydrique réduit significativement l'assimilation en carbone des forêts tempérées (Chaves et al., 2009 ; Barber et al., 2000), qui, notamment, est à relier à une fermeture stomatique prolongée. On estime ainsi, en Europe, à 30 % la perte de production primaire brute due à la sécheresse historique d'août 2003 (Ciais et al., 2005). En parallèle, le déficit hydrique augmente le risque de cavitation et peut induire une perte de fonctionnalité du xylème (Stout & Sala, 2003). Les conséquences peuvent être graves pour l'arbre : l'alimentation en eau des parties distales se voit réduite, altérant leur physiologie et pouvant conduire, à terme, au dessèchement de branches complètes (Cochard et al., 1996). Le stress hydrique modifie également l'allocation du carbone entre croissance des feuilles, des racines et du bois, stockage des glucides, production des métabolites

secondaires et fructification, et ce, pendant plusieurs années après l'aléa (DeLucia et al., 2000 ; Maherali et al., 2001). De plus, à la suite d'une sécheresse, l'arbre devant distribuer ses réserves entre demandes de réparation, d'entretien, de croissance et de défense, toute demande supplémentaire sur ses réserves, déjà limitées par l'aléa, augmente sa vulnérabilité aux stress secondaires comme une autre sécheresse, une canicule, un gel, les dégâts d'insectes ou de pathogènes (Breda et al., 2006). Chaque aléa interagit donc avec les autres au travers de la physiologie de l'arbre et, potentiellement, leurs dommages s'amplifient mutuellement de façon non linéaire (Seidl et al., 2017).

1.2. ... à la démographie

Chacune des répercussions précédemment énoncées, pouvant être également liée à des stress secondaires, a des impacts directs sur les processus démographiques des peuplements forestiers que sont la croissance, la reproduction et la survie (Griffith et al., 2016). Ainsi, on observe que les sécheresses prolongées et les canicules sont reliées à : (1) une diminution du potentiel de croissance ; la croissance radiale et la surface foliaire étant souvent réduites pendant plusieurs années à la suite d'une sécheresse sévère (Zhao & Running, 2010 ; Le Dantec et al., 2000 ; Battaglia et al., 1998) ; (2) une modification de l'effort reproducteur (sûrement le processus le moins étudié) : certains auteurs rapportent une stimulation de la production de fleurs et de graines souvent suivie par une diminution lors des années suivantes (Innes, 1994), pendant que d'autres notent une diminution du seuil de taille à partir duquel la reproduction débute dans un environnement plus sec (Santos-del-Blanco et al., 2013) ; (3) l'initiation de dépérissements (Dobbertin, 2005 ; Galiano et al., 2011) et l'augmentation des risques de mortalité (Adams et al., 2017 ; Allen et al., 2010 ; Anderegg et al., 2013). Notons ici que les dommages induits par la sécheresse entraînent des dysfonctionnements des organes, mais ils n'entraînent que rarement une induction directe et immédiate du dépérissement et de la mortalité des arbres (Breda et al., 2006). En effet, le processus qui mène à la mort d'un arbre est, le plus souvent, le résultat de l'accumulation, sur plusieurs années, des dommages (mécaniques et physiologiques) de multiples événements de stress de natures et d'intensités variées (Manion 1991), associés à des facteurs de sensibilité liés à (1) l'environnement local de l'arbre (LAI du peuplement, pédologie, etc.), (2) à des cofacteurs liés à sa taille ou encore à son âge, ainsi qu'à (3) ses

performances génétiques individuelles dépendantes (Fig. 4) (Martínez-Vilalta et al., 2012 ; Mérian & Lebourgeois 2011 ; Mérian & Lebourgeois 2013 ; Metz et al., 2016).

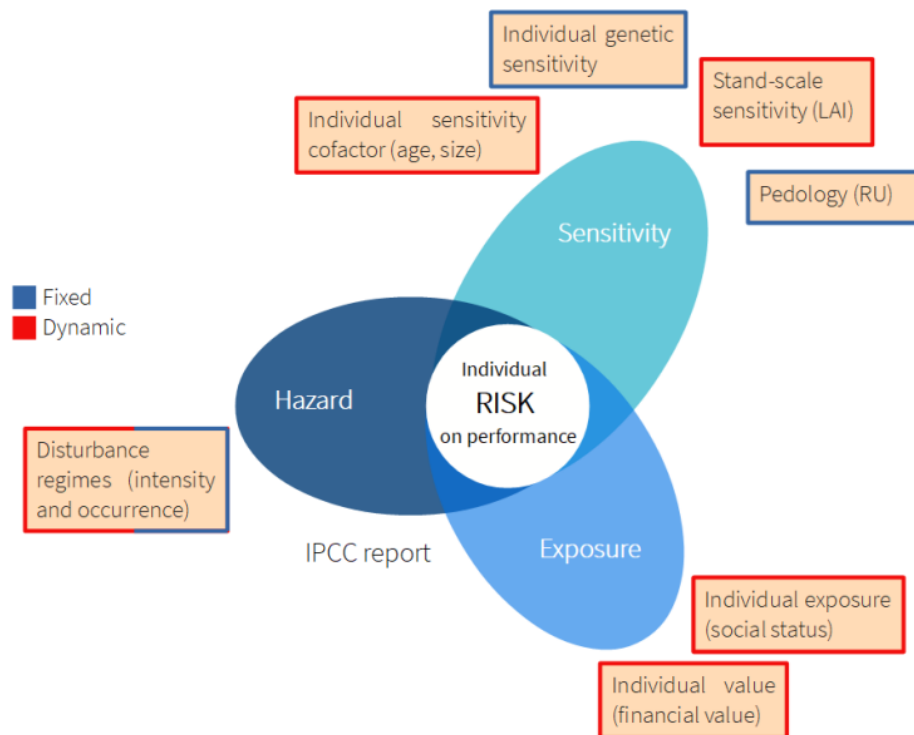


Figure 4. Décomposition du risque sur les performances individuelles d'un arbre (croissance, survie, reproduction) lié à l'aléa sécheresse. Les facteurs modulant les sensibilités identifiées sont (1) à l'échelle de l'arbre : la taille et l'âge de l'arbre ainsi que ses performances génétiques ; (2) à l'échelle du peuplement : la surface foliaire spécifique (LAI) et la réserve utile du sol (RU). Le statut social est identifié comme facteurs d'exposition modulant également l'impact. Notez que la capacité d'adaptation n'est pas considérée à cette échelle de temps puisque le risque présenté ici est centré sur l'individu.

2. Article 3 (publié). Within and between population phenotypic variation in growth vigor and sensitivity to drought stress in five temperate tree species

L'ensemble des processus démographiques (croissance, survie et reproduction) sont directement impactés par les perturbations. Toutefois, mon travail s'est ici concentré sur la fonction de croissance. Si la croissance est directement liée à la productivité forestière, le choix d'en faire le point d'entrée de mes travaux s'explique par la relation étroite qui relie les performances de croissance des arbres à leur valeur sélective et fonctions biologiques en forêt. En effet, le succès reproducteur (Greene & Johnson, 1994 ; Burczyk et al., 1996), la sensibilité à la compétition et aux aléas (Caspersen et al., 2011 ; Bennett et al., 2015) sont tous dépendant de la taille de l'arbre. En outre, le sylviculteur se base notamment sur la surface terrière du peuplement et sur la taille des arbres individuels pour ses choix d'éclaircies. Tous ces éléments font de la croissance un processus particulièrement structurant des interactions entre les pratiques de gestion, les processus démographiques et les perturbations.

Le contenu de cette section correspond à un article dont l'objectif est de formaliser la notion de régime d'impact sécheresse sur la croissance d'une part, et, d'autre part, analyser la variation phénotypique intra-population de la sensibilité et sa relation avec la vigueur. J'ai tiré partie du modèle écophysologique forestier CASTANEA (Dufrêne et al., 2005 ; Davi & Cailleret 2017) ainsi que des données dendrochronologiques individuelles, dendrométriques peuplements, et pédoclimatiques du réseau RENECOFOR⁶. Dans l'objectif de rendre ce travail plus généralisable, j'ai étendu l'étude au-delà des espèces cibles de ma thèse en incluant cinq espèces au total, y compris le sapin Douglas. L'article est publié dans la revue *Forest Ecology and Management*⁷. En tant que premier auteur, j'ai conçu la méthode originale proposée, réalisé les analyses, réalisé les figures et rédigé entièrement la première version de l'article.

⁶ Le réseau RENECOFOR est le REseau National de suivi à long terme des ECOSystèmes FORestiers. Ce réseau a été créé par l'Office national des forêts (ONF) et vise à l'observation et au suivi de 102 sites permanents depuis 1992.

⁷ <https://doi.org/10.1016/j.foreco.2022.120754>

Les résultats mettent en évidence (1) une large variation interindividuelle en termes de sensibilité et de vigueur (des variances intra-population plus élevées que les variances inter-population) et (2) une corrélation positive générale entre la sensibilité et la vigueur individuelle révélant un potentiel compromis de performance de croissance. L'importance de considérer ce compromis et globalement la variation phénotypique de vigueur et de sensibilité dans les décisions de gestion est discutée dans le cadre de l'adaptation au changement climatique.

Within and between population phenotypic variation in growth vigor and sensitivity to drought stress in five temperate tree species

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Abstract

Within-population variation in individual tree growth and response to climate has an impact on forest dynamics, resilience and adaptation to environmental change.

Combining dendrochronological analyses with a process-based ecophysiological model simulating drought stress at the stand scale, we studied the phenotypic variation of two growth-related traits within 22 pure stands of five contrasted tree species sampled in the RENECOFOR network over a wide range of ecological conditions. First, we computed the annual stress level from soil, climate and stand inventory data. Second, we computed individual sensitivity as the quantitative growth response to drought stress level and individual vigor as the capacity to grow in favorable years relative to an average stand-level growth model. We analyzed within-population variation and covariation of individual vigor and sensitivity, their temporal changes during stand development, as well as the effect of environmental conditions on population-level means, variances and correlation.

Our results show that within-population variances in sensitivity and vigor exceed the between-population variances for all species. The populations located in more stressful environments, i.e., low summer precipitation and extractable soil water, showed lower mean and variance of sensitivity, suggesting possible multiscale adaptation at the population level and within populations. None of the environmental factors considered had an effect on the average population vigor or on the within-population variance of vigor. We found a general positive correlation between individual growth sensitivity and vigor in 17 out of 22 populations, potentially revealing a growth performance trade-off. The correlation was more pronounced in low extractable soil water environments, which may be related to a need for stressful conditions to reveal the trade-off or be the consequence of adaptive processes, i.e., acclimation and selection.

If high within-population stand phenotypic variation in growth traits contributes to the resilience and adaptive capacity of forests to climate change, a trade-off could represent a constraint on selection. We provide genetic and environmental arguments supporting the hypothesis of a trade-off, then we highlight the importance of integrating it into the management process, especially during selective thinning, to avoid indirectly increasing population sensitivity by selecting the most vigorous trees.

Keywords

Growth–climate relationships; Drought stress; Forest dynamics; Tree rings; Dendro-phenotypes; Plasticity

1. Introduction

Climate change is associated with increasing drought stress in all forest biomes around the world (Allen et al., 2010; Choat et al., 2012; Allen et al., 2015), with a potentially major impact on their role as carbon sinks (Ma et al., 2012; Anderegg et al., 2015). Drought stress reduces tree growth (Lempereur et al., 2015) and photosynthesis (Cornic & Massacci 1996), and when drought is intense and/or long, drought stress can cause hydraulic failures and lead to defoliation and tree death (Brodrigg & Cochard 2009). Tree rings analysis is a widely recognized approach to assess the effect of climate on tree growth (Fritts, 1971, Cook, 1985, Giguère-Croteau et al., 2019) and detect early-warning signs of mortality (Cailleret et al., 2019). Dendroecological approaches proved successful in investigating the impact of drought stress on the average radial growth of stands or cohorts and highlighting important variations in this impact with life history traits (DeSoto et al., 2020), social status (Mérian & Lebourgeois, 2011), stand structure and geographical location within the species distribution range (Camarero 2021). Moreover, introducing the interindividual variability in tree-ring–climate relationships allows for a more in-depth assessment of the effect of climate on stand growth that could improve the quality of ecological inferences (Carrer et al., 2011).

Within-population interindividual phenotypic variation of growth results from the combination of extrinsic factors, such as resource availability and competition, and intrinsic factors, such as genotype, acclimation, microsite, age, size and social status (Aranda et al., 2010; Corcuera et al., 2011). In the context of climate change, two growth traits are useful to distinguish: the sensitivity to drought stress, i.e. the response of tree growth to stress level, and the growth potential, hereinafter referred to as vigor. Sensitivity and vigor both contribute to tree size and therefore to competitive and possibly reproductive performances. In comparison to the precisely defined drought sensitivity and its extensive use in ecophysiological and dendrometrical studies, vigor has been defined more loosely and mainly used in applied genetic studies with little consideration of stand dynamics effects. Within-population variation and covariation of individual vigor and sensitivity to drought are factors of resilience in the face of climate change. Phenotypic variations in drought tolerance may buffer the short-term impacts

of drought on the ecological functions of forests (Bréda et al., 2006; Aitken et al., 2008; Grady et al., 2011; Alfaro et al., 2014). In the long term, within-population variance and correlations of growth traits determine their take on selection and the evolutionary potential of populations. On different time scales, acclimation and selection are likely to jointly influence the sensitivity and vigor of the populations as well as the phenotypic variation, with both processes being subject to local environmental constraints. Previous works revealed the genetic basis of within-population variation for sensitivity to climate (Liepe 2014; Bansal et al., 2015; Depardieu et al., 2020).

Among tree populations, a genetic trade-off between vigor and sensitivity to climate has been reported in multisite common garden experiments: those populations that grow better in favorable sites generally grow less than others in stressful conditions (e.g., *Pinus contorta* and *P. sylvestris* in Rehfeldt et al., 2001; 2002). The genetic component of this trade-off may result from a balancing selection process for contrasting ecological strategies, such as a water economy strategy in which plants maintain low growth rates and low rates of gas exchange during droughts or a water uptake strategy in which plants have more rapid instant growth through higher rates of gas exchange when water is available, allowing them to complete important biological functions before drought onset (Arntz & Delph 2001). At the within-population scale, a phenotypic trade-off between vigor and sensitivity was observed in *Abies alba* by Nourtier et al., (2014) and in *Cedrus atlantica* by Fallour-Rubio et al., (2009). In a *Fagus sylvatica* population facing summer droughts, Bontemps et al., (2017) observed phenotypic trade-offs in the phenology, growth dynamics and anatomy among trees related to vigor and sensitivity. This trade-off can be due to environmental variability: individuals with higher water resources are expected to be more vigorous but also more sensitive to drought stress (Nourtier et al., 2014; Cailleret et al., 2019). Within-population trade-offs may also be under genetic control, which could explain the changes in correlation observed between cohorts within a single *Cedrus atlantica* forest (Fallour-Rubio et al., 2009).

Ring width data provide repeated growth measures over time, i.e., under different climates, of the trees that survived competition and hazards until sampling. Hence, they are very valuable data for disentangling individuals from environmental effects on growth vigor and sensitivity *in situ*, which can

be achieved by using an individual-based growth analysis model that explicitly considers the factors of tree age, size, social status, the overall site environment and an individual random effect that captures the genetic and microsite effects (Fallour-Rubio et al., 2009). Additionally, tree growth vigor and sensitivity to drought stress need to be considered dynamic phenotypic traits (Peltier & Ogle, 2020). Indeed, these traits are driven not only by static factors such as tree genotype or microsite conditions but also by dynamically changing factors such as tree age, size and social status (Cook, 1985; Trouvé et al., 2014; Perin et al., 2017; Forrester, 2019; Peltier & Ogle 2020; Mašek et al., 2021). These individual features may change drastically over the potential long lifespan of trees in relation to stand development and forest management. To our knowledge, however, no study to date has combined a growth analysis model at the tree scale with a dynamic perspective of vigor and sensitivity.

Another challenge when investigating tree growth sensitivity to environmental stress is to qualify and quantify the stress level. Some approaches, such as the resistance, recovery and resilience indices proposed by Lloret et al., (2011), bypass the quantitative level of stress and focus on the temporal sequence of growth variation. In this way, Depardieu et al., (2020) estimated within-population genetic variation in Lloret indices based on common garden experiments. However, in natural stands, this approach raises the question of comparability between individuals, sites and species, since the observed response is specific to a given water stress level in a given background stress, both of which are often not measured (Schwarz et al., 2020). Other dendroecological studies explicitly consider the individual pedoclimatic variables driving intra- and interannual variation in tree growth (e.g., Fritts, 1971, Mérian et al., 2011). As it can be challenging to generalize the relation between tree-ring widths and any single pedoclimatic variable, another related approach consists of using synthetic drought indices, such as the Palmer drought severity index or standardized precipitation evapotranspiration index (PDSI: Palmer, 1965; SPEI: Vicente-Serrano et al., 2010). Such indices precisely account for the environmental factors of stress but are irrespective of the physiological reaction of the plant and neglect the crucial importance of soil properties, stand density and species functional traits, which may either amplify or buffer drought stress. In other words, they may not appropriately inform the effective intensity and duration of drought stress (Zang et al., 2020).

In this study, we combined dendrochronological analyses with an ecophysiological process-based model assessing the drought stress level and an individual-based growth model to investigate the phenotypic variation in growth sensitivity and vigor. We took advantage of the RENECOFOR dataset, an extensive tree-ring dataset that includes 61 pure stands of five temperate tree species, i.e., *Fagus sylvatica*, *Pseudotsuga menziesii*, *Pinus pinaster*, *Quercus petraea* and *Quercus robur*, sampled over a wide range of ecological conditions, thus covering a broad range of climate–growth relationships that have been shown to vary among species, stands and social cohorts (Lebourgeois et al., 2005, Lebourgeois et al., 2010, Mérian et al., 2011; Mérian & Lebourgeois, 2011; Guillemot et al., 2015). More specifically, in this study, we sought (1) to quantify the variance of growth sensitivity and vigor within forest tree populations, (2) to assess the correlation between these traits and, in particular, test for a possible trade-off, (3) to characterize the temporal dynamics of variances and correlation within populations, and (4) to identify pedoclimatic environmental factors that explain differences in variances, correlation, and average values of growth sensitivity and vigor among populations.

Here, we defined individual vigor as the growth performance in favorable years, and sensitivity as the reaction norm of growth to stress level. For both traits, we sought to capture an individual effect independent of cofactors such as age or size. We hypothesize that genetic and micro-environmental factors may jointly contribute to the observed variation in sensitivity and vigor at the individual tree level. We consider that phenotypic variation and covariation of growth sensitivity to drought and vigor directly influence forest stand dynamics and forest management choices and, therefore, interfere with selection through size-dependent reproductive success (Greene & Johnson, 1994; Burczyk et al., 1996), growth and survival (Caspersen et al., 2011; Bennett et al., 2015).

2. Material and methods

2.1. Study area and species

Our study is based on the French permanent plot network for the monitoring of forest ecosystems (RENECOFOR, part of the ICP Forests Level II network, Lorenz 1995). We focused here

on five contrasted species (i.e., contrasted autecology, gymnosperm vs. angiosperm, shade tolerant vs. intolerant, high vs. low growth rate) sampled in 61 forest tree populations managed in pure and even-aged stands: *Fagus sylvatica* L. ($n = 20$ populations), *Pseudotsuga menziesii* (Mirb.) Franco ($n = 6$), *Pinus pinaster* Aiton ($n = 7$), *Quercus petraea* (Matt.) Liebl. ($n = 19$) and *Quercus robur* L. ($n = 9$). Together, the five temperate species represent 43% of the French standing volume (IGN, 2021). The 61 populations were located between $41^{\circ}45'08''$ and $50^{\circ}10'16''$ N and between $3^{\circ}32'34''$ and $9^{\circ}12'23''$ W (Fig. 1) and covered a wide range of bioclimatic conditions: oceanic ($n = 15$ populations), semi-continental ($n = 35$), Mediterranean ($n = 2$) and mountainous ($n = 11$).

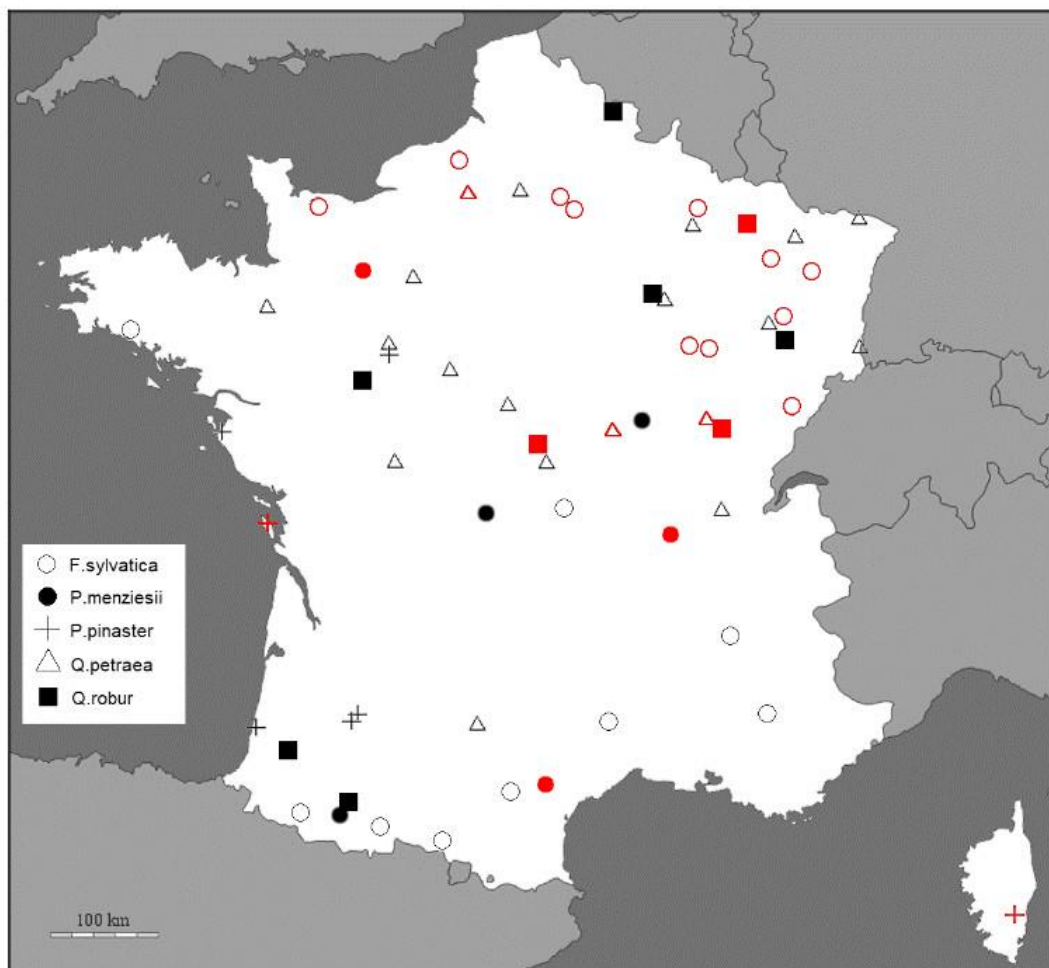


Figure 1. Geographical position of the 61 forest tree populations in the RENECOFOR network (ICP Forests Level II network) for the five species studied. The 22 populations selected for analysis are in red (see 2.4. Selection of populations and temporal intervals for analyses).

Over the 1959–1994 period, the mean annual precipitation varied from 647 to 1441 mm per year among populations. The mean minimum and the mean maximum temperature ranged from 4.2 °C to 10.1 °C and 9.6 °C to 17.3 °C, respectively. The elevation ranged from 5 to 1400 meters above sea level, and the slope ranged from 0 to 55%. The populations sampled above an altitude of 500 meters ($n = 13$) were mainly *F. sylvatica* and *P. menziesii*. Conversely, *P. pinaster*, *Q. robur*, and *Q. petraea* were mostly sampled on plains. We computed the extractable soil water for trees (*ESW*) as follows:

$$ESW = D (1 - C)(\theta_{fc} - \theta_{wilt}) \quad (\text{equation 1}),$$

where D is soil depth, C is the coarse element percentage, θ_{wilt} is humidity at the wilting point and θ_{fc} is humidity at field capacity assessed using soil texture data (Baize & Jabiol 1995; Supp. Table 1). The *ESW* computed over the entire soil profile ranged from 19 to 351 mm among populations.

2.2. Selected trees, ring-width measurements and analysis

We used tree coring data obtained in 1995 by Lebourgeois et al., (1997). Briefly, within each population, 23 to 30 dominant and codominant trees were cored at breast height as close as possible to the pith with an increment borer. Ring widths were measured with a stereomicroscope connected to a microcomputer and the tree ring program SAISIE (Becker, 1989) to the nearest 0.01 mm. Then, the individual ring width series were cross-dated by detecting regional pointer years and checked for erroneous dating (Lebourgeois et al., 2005).

Tree-ring widths generally show a pronounced trend to change with tree size and age as well as with stand structure and competition (Trouvé et al., 2014; Perin et al., 2017). In this study, to disentangle the effect of climate on radial growth from the effect of other factors unrelated to climate, we standardized the individual radial growth series using a 30-year cubic smoothing spline with a 50% frequency response cutoff (Cook & Peters, 1981; Mérian & Lebourgeois, 2011). The transformation from the original ring width to the ring width index (*RWI*) was as follows:

$$RWI = W_{original}/W_{trend} \quad (\text{equation 2}),$$

where $W_{original}$ is the original tree ring width and W_{trend} is the ring width trend unrelated to climate identified by the spline function. The standardized individual series were averaged using a bi-weighted robust mean to create stand tree-ring chronologies (Cook & Peters 1981).

All core data processing was undertaken using the Dendrochronology Program Library (dplR; Bunn, 2008) in R version 3.6.2 (R Development Core Team, 2019).

2.3. Simulation of the edaphic drought stress level

An appropriate approach to quantify water stress is key for any type of growth responses analysis as the drought index choice may strongly influence the results (Van Loon et al. 2016). Raw climate data, as well as the PDSI or SPEI index, are valuable indicators for the study of drought on large scales but do not capture the intensity and duration of site-specific soil water deficits (Zang et al. 2020). For these reasons, we opted for an ecophysiological approach and exhaustivity quantified water reserves and flux within each plot.

We used an ecophysiological process-based model (CASTANEA, Dufrêne et al., 2005; Davi & Cailleret 2017) to simulate the annual drought stress level relative to the soil water content experienced by trees (*StressLvl*). We set the soil forcing variables (soil depth, texture, coarse element percentage) using the plot soil values available in the RENECOFOR dataset. We extracted the daily local climatic variables (minimum, average and maximum temperatures; precipitation; wind speed; average relative humidity; global radiation) from the objective analysis module SAFRAN (Durand et al., 1993; Vidal et al., 2010) using the closest grid points to the sampled populations (8 km grid resolution, data available from 1959 to 2019). We initialized the dendrometric variables, i.e., the number of trees per hectare (*Nha*) and the mean diameter at breast height (*DBH*), using the stand dendrometric values available in the RENECOFOR dataset. The parameters used for the simulations and their values are given per species in Supplementary Table 2.

We computed daily soil water content based on supply and demand dynamics applied to soil moisture and as a function of soil forcing variables. Campbell's soil water retention equation (Campbell,

1974) was used to predict the soil water potential (Ψ_{soil}) at a given volumetric water content (θ) anchored at the saturated volumetric water content (θ_{sat}) as:

$$\Psi_{soil} = \Psi_e \left(\frac{\theta}{\theta_{sat}} \right)^{-b} \quad (\text{equation 3}),$$

where Ψ_e is the air-entry matric potential and b is the soil water retention parameter. Ψ_e , b and θ_{sat} are strongly dependent on soil texture, and we assessed their local values using soil texture data (Bonan, 2019; Supp. Table 1).

Then, we used CASTANEA to integrate the annual soil water balance (Dufrêne et al., 2005) in the form of a drought stress level indicator (*StressLvl*) computed as a Palmer index measured in MPa (Palmer, 1965):

$$\text{StressLvl} = \sum_{d=1}^{365} \Psi_{soil} \quad (\text{equation 4}),$$

where Ψ_{soil} is the daily soil water potential of day d .

Thus, *StressLvl* integrates both the duration and intensity of the annual water deficit. Subsequently, we used the *StressLvl* time series simulated with CASTANEA to characterize the interannual variation in drought stress in each studied population.

2.4. Selection of populations and temporal intervals for analyses

To study the temporal dynamics of growth sensitivity and vigor, we defined 21-year moving intervals slipped by one year. The 21-year period represented a compromise between the temporal resolution required to reveal variations in growth performance and the minimum number of years required to observe sufficient annual variation in *StressLvl* and growth. Here, we eliminated populations whose tree-ring time series was less than the interval length of 21 years. The youngest selected populations show only a few temporal intervals.

The growth response to drought stress may be masked by other biotic, abiotic or anthropogenic disturbance factors. These factors may differ among species and populations, making it difficult to disentangle and quantify *a posteriori* (Galván et al., 2014). For these reasons, we carried out a double

selection of populations and temporal intervals and retained only populations and intervals for which the growth response to drought stress was directly observable. To do so, we selected populations with a significant simple correlation between stand tree-ring chronology and *StressLvl* over the whole period of observation ($p < 0.05$) and the temporal intervals of these populations with a significant simple correlation between stand tree-ring chronology and *StressLvl* ($p < 0.05$). For some populations ($n = 14$), the correlation between *RWI* and *StressLvl* was not significant overall but significant for some temporal intervals; we still eliminated them. This selection process also led us to discard populations and intervals with low interannual drought stress variability or for which water was not a factor limiting growth.

Among the 61 initial populations, 22 met the selection criteria and were used for the analyses (Fig. 1): 11 *F. sylvatica* populations (55%), 3 *P. menziesii* (50%), 2 *P. pinaster* (29%), 3 *Q. robur* (33%) and 3 *Q. petraea* (16%). The geographical position of the 22 selected populations is highlighted in Figure 1. The climatic and pedological ranges of the selected populations were close to those of the initial group: mean annual rainfall ranged from 686 to 1422 mm among selected populations; mean minimum and mean maximum temperature ranged from 5.6 °C to 10.1 °C and 11.9 °C to 16.4 °C, respectively; and extractable soil water for trees ranged from 19 to 275 mm (Supp. Table 3). The average population age in the selected temporal intervals varied between 13 and 183 (Supp. Table 3), which provided a contrasting population panel to analyze the variation of the studied traits.

2.5. Growth sensitivity to drought stress and vigor

We first estimated individual growth sensitivity and vigor within each selected temporal interval and then computed mean values over the selected intervals both at the individual tree level within each population and at the population level.

2.5.1. Sensitivity estimation

For each tree of each population and at each selected temporal interval *T*, we computed the regression coefficient between the ring width index (*RWI*) and *StressLvl* simulated with CASTANEA as a quantitative estimate of individual growth sensitivity to drought stress. We used the following linear model to estimate individual sensitivity within each selected temporal interval *T* (*TSensi*):

$$RWI_{i,n} = \beta + TSensi_i \times StressLvl_n + \varepsilon_{i,n} \quad (\text{equation 5}),$$

where β is the intercept, $TSensi$ is the temporal growth sensitivity to drought stress, $StressLvl$ is the annual drought stress simulated by the process-based model, and ε is the between-year growth residual. Subscripts i and n denote the individual and the year considered, respectively.

2.5.2. Vigor estimation

We computed individual vigor on a subset of the data corresponding to the three years of lowest $StressLvl$ within each selected 21-years interval, as follows.

For pure even-aged stands, growth models, in which annual growth is a function of DBH, had been developed for *F. sylvatica* (Dhôte 1991; Dhôte & Le Moguedec 2012), *Quercus sp.* (Dhôte & Le Moguedec 2012; Trouvé et al., 2014), *P. menziesii* (Deleuze et al., 2004; Trouvé et al., 2014; Perin et al., 2017) and *P. pinaster* (Najar et al., 1999). In these empirical models, the relationship between DBH and radial growth dynamically evolves with stand structure. Here, for each of the three years, we assumed a linear relation of radial growth to DBH, and we defined individual vigor as the deviation from this average growth model, so vigor is independent of initial tree size. The populations of the RENECOFOR network are, for the most part, managed in even-aged stands (Mérian & Lebourgeois, 2011). However, few ones are likely to deviate from even-aged structure. Therefore, we systematically added age as an explanatory factor in the model. Thus, we analyzed the 3-year subdataset within each interval with the following model:

$$Woriginal_{i,n} = \beta + \tau_n + DBH + \tau_n:DBH + Age_i + TVig_i + \varepsilon_{i,n} \quad (\text{equation 6}),$$

where $Woriginal_{i,n}$ is the original ring width of tree i in year n , β is the intercept, τ_n is the effect of year n on growth, DBH is the effect of DBH, $\tau_n:DBH$ is the interaction between DBH and year, Age_i is the average age of tree i in the considered interval, $TVig_i$ is the temporal vigor of tree i in the considered interval, and $\varepsilon_{i,n}$ is the residual variation for the i th tree in the n th year. We used individual overbark DBH of year n (see Perin et al., 2017), computed from the cumulative ring widths from the inside out until year n . For the few populations deviating from even-aged, collinearity is possible between DBH and Age , but it does not affect the estimation of vigor.

2.4.3. Sensitivity and vigor: from dynamic variables to intrinsic individual and average population values

To characterize each individual by unique values, we computed the individual intrinsic growth sensitivity (*ISensi*) and vigor (*IVig*) for each individual of each population as the mean of its sensitivity and vigor values over the selected intervals. We computed the average population sensitivity (μ *Sensi*) by averaging the intrinsic sensitivity of individuals and the average population vigor (μ *Vig*) by averaging individual growth in favorable years. In addition, based on the average population sensitivity and vigor, we computed the between-population variances for each species and over all species as references to which we compared the within-population variances. Finally, to quantify the correlation between growth sensitivity and vigor, we computed the Pearson correlation coefficient between intrinsic vigor (*IVig*) and sensitivity (*ISensi*) for each population and between temporal dynamic growth sensitivity (*TSensi*) and vigor (*TVig*) for each interval. Table 1 lists all the growth variables and their associated variances and correlations.

Table 1. Glossary of the growth variables and associated variances and covariances analyzed in this study.

Full Name	Code	Unit	Description
Temporal vigor	<i>TVig</i>	cm	A temporal dynamic variable quantifying the specific ability of a tree to grow in favorable years relative to an average growth model
Intrinsic vigor	<i>IVig</i>	cm	The averaged value of <i>TVig</i> over temporal intervals
Average population vigor	μ <i>Vig</i>	cm	The average growth of populations during favorable years
Variance of temporal vigor	<i>var (TVig)</i>	cm ²	The variance of temporal vigor
Within-population variance of vigor	<i>var (IVig)</i>	cm ²	The variance of intrinsic vigor
Within-species between-population variance of vigor	<i>var (μVig/sp)</i>	cm ²	The within-species variance of average population vigor
Between-population variance of vigor	<i>var (μVig)</i>	cm ²	The total variance of average population vigor over all species
Temporal sensitivity	<i>TSensi</i>	MPa ⁻¹	A temporal dynamic variable quantifying the specific response of a tree's growth to drought stress level
Intrinsic sensitivity	<i>ISensi</i>	MPa ⁻¹	The averaged value of <i>TSensi</i> over temporal intervals
Average population sensitivity	μ <i>Sensi</i>	MPa ⁻¹	The average population sensitivity obtained by averaging the individual intrinsic sensitivities
Variance of temporal sensitivity	<i>var (TSensi)</i>	MPa ⁻²	The variance of temporal sensitivity
Within-population variance of sensitivity	<i>var (ISensi)</i>	MPa ⁻²	The variance of intrinsic sensitivity

Within-species between-population variance of sensitivity	$var(\mu Sensi/sp)$	MPa^{-2}	The within-species variance of average population sensitivity
Between-population variance of sensitivity	$var(\mu Sensi)$	MPa^{-2}	The total variance of average population sensitivity over all species
Correlation between temporal sensitivity and vigor	$r(TVig, TSensi)$	-	The Pearson correlation coefficient between temporal vigor and temporal sensitivity
Within-population correlation between sensitivity and vigor	$r(IVig, ISensi)$	-	The Pearson correlation coefficient between intrinsic vigor and intrinsic sensitivity

2.6. Statistical analysis between populations

We used mixed models to study the overall effects of local environmental conditions (climate and soil) and average population age across species and sites on population means, variances and correlations between growth sensitivity and vigor. For each of these variables, we built a model with 1959–1994 average summer precipitation and maximum temperature (in June, July, and August), extractable soil water and average population age in the selected intervals as explanatory variables. We added the species as a random cofactor in the model. The retained models were:

$$Y_p = \beta + Pr_p + Tmax_p + ESW_p + age_p + sp_p + \varepsilon_p \quad (\text{equation 7}),$$

where Y successively corresponds to $\mu Sensi$, $var(ISensi)$, $var(IVig)$ and $r(IVig, ISensi)$; β is the intercept; Pr and $Tmax$ are the 1959–1994 average summer precipitation and maximum temperature, respectively; ESW is the extractable soil water; age is the average population age in the selected intervals; sp is the species random cofactor; and ε is the between-population Y residual. Subscript p denotes the population. Specifically, for the average population vigor (μVig), we added tree density (Nha , a proxy for competition; Supp. Table 3) as explanatory variables since growth is largely dependent on competition level:

$$\mu Vig_p = \beta + Pr_p + Tmax_p + ESW_p + Nha_p + age_p + sp_p + \varepsilon_p \quad (\text{equation 8})$$

We performed all statistical analyses using R version 3.6.2 (R Development Core Team, 2019).

3. Results

3.1. Within-population variations in growth sensitivity and vigor

Within each species, within-population variance of sensitivity (resp. vigor) represents on average 520% (resp. 376%) of the between-population variance. Considering all species together, the mean within-population variance of sensitivity (resp. vigor) represents 47% (resp. 17%) of the between-population variance over all populations from all species (detailed variances are given in Supp. Table 4). These results indicate that most of the phenotypic variation in vigor and sensitivity to drought stress is within populations.

Among the twenty-two populations, the correlation between intrinsic sensitivity and vigor was significantly positive in ten populations at threshold $p < 0.05$ and in three populations at threshold $p < 0.1$, which included 7 *F. sylvatica* populations (64%), 2 *P. menziesii* (67%), 1 *P. pinaster* (50%), 2 *Q. robur* (67%), and 1 *Q. petraea* (33%) (Fig. 2 for *P. menziesii* and Supp. Fig. 1 for the other species). In these 13 populations, individual trees with better vigor showed higher growth sensitivity to drought stress. No significant negative correlation was observed. It should be noted that some trees, for the most part the less vigorous ones, were insensitive to drought stress, i.e., $ISensi \leq 0$.

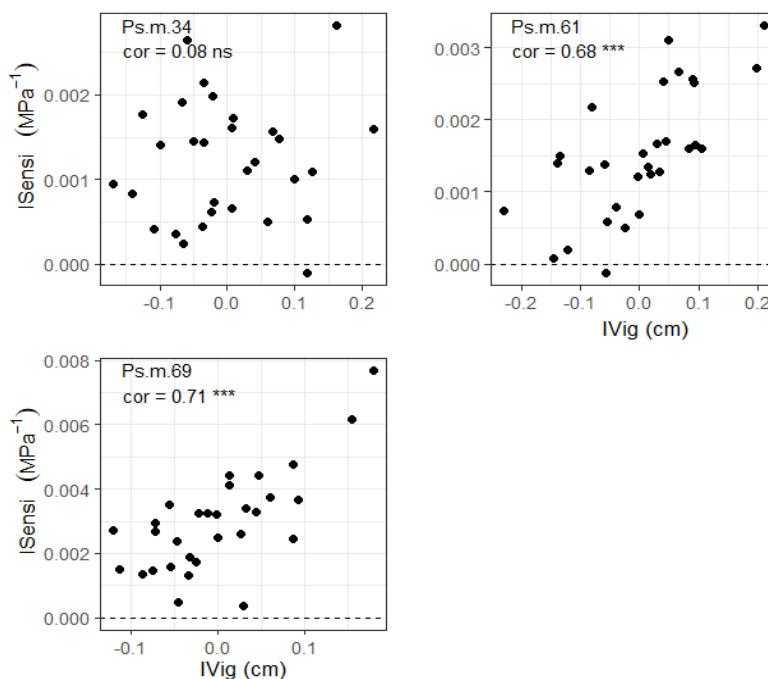


Figure 2. Correlation between intrinsic sensitivity (*ISensi*) and intrinsic vigor (*IVig*) in the three *P. menziesii* populations (Ps.m 34, Ps.m 61 and Ps.m 69). Each point represents an individual tree. The correlation was significantly positive in two of the three populations (Ps.m 61 and Ps.m 69). The significance level is indicated on the graphs by '****' at $p < 0.001$, '***' at $p < 0.01$, '*' at $p < 0.05$, '.' at $p < 0.1$ and 'ns' above. The dotted lines indicate zero sensitivity. Note that some trees were insensitive, i.e., $ISensi \leq 0$.

We observed a temporal variation in the variance of sensitivity and vigor: the temporal variations within populations did not overcome the largest differences between contrasted populations and did not show a clear common pattern among populations or species (Fig. 3a,b for *P. menziesii* and Supp. Fig. 2 for the other species). The value and significance of the correlation coefficients between growth sensitivity (*TSensi*) and vigor (*TVig*) also varied among temporal intervals without a clear pattern (Fig. 3c). Nevertheless, the correlation was positive for most populations and intervals (Fig. 3c for *P. menziesii* and Supp. Fig. 2 for the other species). We found at least one significant positive correlation between temporal sensitivity and vigor within 17 of the 22 selected populations and no significant negative correlation. We observed this correlation in populations at the juvenile stage (e.g., <15 years in Ps.m 69) as well as in largely mature populations (e.g., >180 years in Q.r 55).

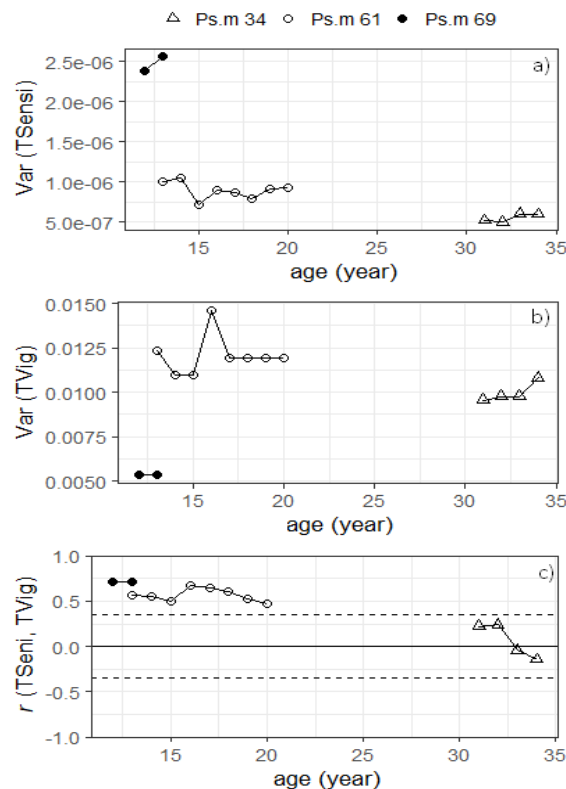


Figure 3. Variances (a, b) and correlation (c) of temporal sensitivity (*TSensi*) and temporal vigor (*TVig*) for each interval T of the three *P. menziesii* populations (Ps.m 34, Ps.m 61 and Ps.m 69). Each point represents an interval T characterized by the average age of the trees (*age*). On the graph c, the dashed lines represent the values beyond which correlation coefficients are significant at $p < 0.05$ computed for a sample size of $n = 30$ individuals.

3.2. Effect of environmental conditions of the populations on the variations in sensitivity and vigor

Over the entire period from 1959 to 1994, the different populations showed high contrasts in the environmental factors driving water deficits: average summer precipitation (*Pr*) ranged from 116 to 347 mm, average summer maximum temperature (*Tmax*) ranged from 19 to 24 °C, and extractable soil water ranged (*ESW*) from 19 to 275 mm (Supp. Table 3). It should be noted that the range of water conditions varied between species with some overlap: *ESW* varied significantly between species unlike *Pr* and *Tmax*.

Regarding sensitivity to drought stress, summer precipitation (*Pr*; $p < 0.001$) and extractable soil water (*ESW*; $p = 0.009$) had a positive effect on the average population sensitivity (μ *Sensi*), while maximum summer temperature (*Tmax*) and average population age (*age*) had no significant effect (Table 2a; Supp. Fig. 3a,b). The overall model had a marginal R^2 value of 0.56. In addition, summer precipitation (*Pr*; $p < 0.001$) had a positive effect on within-population variance of sensitivity (*var* (*ISensi*)), while extractable soil water (*ESW*), maximum summer temperature (*Tmax*) and average population age (*age*) had no significant effect (Table 2b; Supp. Fig. 3c). The overall model had a marginal R^2 value of 0.56. To summarize, the average population value and the within-population variance of sensitivity to drought stress decreased with greater water constraints.

Regarding vigor, no factor had a significant effect on either average population vigor (μ *Vig*) or on the within-population variance of vigor (*var* (*IVig*)) (Table 2c,d).

Regarding the sensitivity–vigor correlation, extractable soil water (*ESW*; $p = 0.012$) had a negative effect on the within-population correlation between sensitivity and vigor (r (*IVig*, *ISensi*)), while maximum summer precipitation (*Pr*), summer temperature (*Tmax*) and average population age

had no significant effects (Fig. 4; Table 2e). The overall model had a marginal R^2 value of 0.24. These results indicate that environmental factors were a major determinant of the correlation between growth sensitivity to drought stress and vigor within populations.

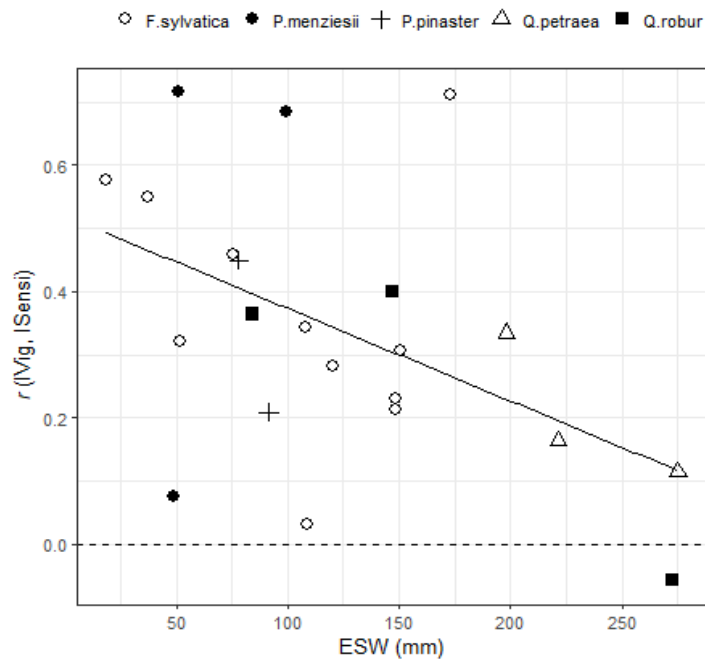


Figure 4. Effect of extractable soil water (ESW) on the correlation between sensitivity and vigor ($r(IVig, ISensi)$). Each point represents a population. The correlation increases with lower ESW . The line shown is the simple regression coefficients on all the selected populations ($n = 22$): $r(IVig, ISensi) = 0.52 - 1.47 \times 10^{-3} ESW$ ($R^2 = 0.24$).

Table 2. Results of the mixed models on all the selected populations ($n = 22$ populations) of average population sensitivity (a), within-population variance of sensitivity (b), average population vigor (c), within-population variance of vigor (d), and within-population correlation between sensitivity and vigor (e) according to average summer precipitation (Pr), average maximum summer temperature ($Tmax$), extractable soil water (ESW), species (sp), stand density (Nha) and average population age (age). Significant results are shown in bold with the significance level indicated by '***' at $p < 0.001$, '**' at $p < 0.01$, '*' at $p < 0.05$ and '.' at $p < 0.1$.

	Source	Estimate	Chisq.	Df	p-Value
a) μ Sensi					
	(Intercept)	6.14×10^{-3}	0.95	1	0.329
	Pr	2.78×10^{-5}	16.87	1	< 0.001 ***
	Tmax	-4.65×10^{-4}	2.56	1	0.110
	ESW	1.23×10^{-5}	6.73	1	0.009 **
	age	2.69×10^{-6}	0.14	1	0.712
b) var (ISensi)					
	(Intercept)	-2.75×10^{-6}	0.16	1	0.687
	Pr	3.50×10^{-8}	22.87	1	< 0.001 ***
	Tmax	-1.27×10^{-7}	0.16	1	0.688
	ESW	8.33×10^{-9}	2.58	1	0.108
	age	-5.55×10^{-9}	0.48	1	0.488
c) μ Vig					
	(Intercept)	1.66×10^{-1}	0.27	1	0.602
	Pr	4.35×10^{-4}	1.15	1	0.284
	Tmax	1.07×10^{-2}	0.49	1	0.483
	ESW	-2.00×10^{-4}	0.36	1	0.548
	age	-1.19×10^{-3}	3.24	1	0.072
	Nha	-5.37×10^{-5}	0.36	1	0.550
d) var (IVig)					
	(Intercept)	2.79×10^{-3}	0.12	1	0.730
	Pr	-1.23×10^{-5}	2.08	1	0.150
	Tmax	5.91×10^{-5}	0.03	1	0.871
	ESW	1.24×10^{-5}	2.68	1	0.102
	age	3.245×10^{-6}	0.09	1	0.761
e) r (IVig, ISensi)					
	(Intercept)	-0.29×10^{-1}	0.10	1	0.753
	Pr	7.08×10^{-4}	0.53	1	0.468
	Tmax	3.36×10^{-2}	0.64	1	0.422
	ESW	-1.70×10^{-3}	6.25	1	0.012 *
	age	-3.12×10^{-4}	0.09	1	0.766

4. Discussion

In this study, we quantified the variation and covariation of vigor and sensitivity to drought, as well as their temporal dynamics, both within and between 22 populations of five contrasting temperate species. We defined two growth variables at the individual tree level as a framework to disentangle the components of tree growth performance in environments with varying drought stress levels. We argue

that these two individual growth variables can be considered new tree-ring based phenotypic traits (Housset et al., 2018).

Our results are based on a subset of the RENECOFOR dataset for which growth response to stress was present (selection of populations and intervals). The pedoclimatic range of all the populations and that of the selected subset were equivalent. We hypothesized that the populations and intervals removed from the analyses experienced insufficient drought stress to observe a growth response and/or were impacted by other disturbance factors masking the relationship between growth and drought stress. Nevertheless, species-specific seasonal growth dynamics may also affect the response to drought. First, the formation of earlywood in ring porous wood species, such as *Quercus sp.*, largely depends on remobilization from reserves accumulated in previous years and starts before budburst (Michelot et al., 2012). In these species, tree rings of similar widths can have very different proportions of latewood (Lebourgeois, 1999). Therefore, wood density can differ considerably from year to year, buffering the variation of ring width in response to environmental conditions over the overall growing period (Schwarz et al., 2020). In this study, we attribute the small proportion of *Quercus sp.* populations selected for analyses (21% compared to 49% for other species) to these physiological and anatomical characteristics and to the fact that the *Quercus sp.* populations are preferentially on the best site conditions in the RENECOFOR network (Lebourgeois, 1999; Mérian et al., 2011). Second, there may be a certain time lag between the growth period and the water stress period, e.g., drought in autumn could deepen the annual water deficit while annual growth would not be affected. The intra-annual analysis of radial growth can help to define the growing season over which to integrate the stress (Olivar et al., 2014). The growing season varies greatly depending on the site and the species (Michelot et al., 2012). Pine species show active growth in October and late regrowth until November (*P. pinaster*, Vieira et al., 2009; *P. halepensis*, Olivar et al., 2014). In oak, growth usually stops at the first events of water deficit, during the months of June-July (*Q. petraea*, Bréda & Granier, 1996). For the sake of comparability between sites and species, we have integrated stress at the scale of the entire year. Thus, our selection of intervals would exclude autumn drought events having no impact on the annual growth.

However, in the temperate region, most of the water stress occurs in July and August, and therefore a moderate impact on the results is expected.

4.1. A notable within-population variation in sensitivity and vigor

Our results reveal high levels of within-population phenotypic variation in growth sensitivity and vigor. On average for all species and for both traits, the within-population variance was higher than the variance of population mean values, even though the different populations of each species were sampled in different geographic areas and different environmental conditions. This suggests both genetic and environmental contributions to between-population variance. We had no information on microenvironmental heterogeneity within each population that could help disentangle the genetic and microenvironmental components of within-population variance, but the environmental characterization at the population level provides a clue on this issue, as follows.

The average population sensitivity was mainly driven by two environmental factors, summer precipitation and extractable soil water (ESW). Summer precipitation also had a positive effect on within-population variance in sensitivity. As a parsimonious interpretation, we can assume that the positive impact of summer precipitation on within-population variance simply results from a scale effect, thus contributing to the environmental component of the variance of sensitivity. In contrast, ESW only drove the average population sensitivity but neither the within-population variance nor the average population vigor. Thus, ESW is likely to explain part of the between-population variance that is not a scale effect, whereby lower sensitivity in populations of lower ESW effectively indicates a lower response to stress. Although we cannot properly test for local adaptation based on our dataset, this cline in sensitivity along the ESW gradient suggests past adaptation to drought stress regimes. Furthermore, it has been shown that microgeographic variation in soil conditions within populations may contribute to interindividual variation in the response to drought (Nourtier et al., 2014) and there is increasing empirical evidence of microenvironmental adaptation within forest tree populations (Audigeos et al., 2013; Heer et al., 2018; Brousseau et al., 2021). Therefore, we also hypothesize that part of the within-population variance in sensitivity, which is higher than between-population variance, is partly under genetic control.

The average population vigor was not affected by any environmental factors. In particular, the lack of effect of summer precipitation indicates that our selection of the most favorable years for computing vigor effectively excluded water-limiting years. None of the environmental factors tested showed an effect on the within-population variance in vigor, indicating in particular that within-population phenotypic variation in vigor was unrelated to drought conditions.

In this study, we considered temporal variations in growth vigor and sensitivity to drought during stand development. For growth-related traits, temporal changes in population means and variances during a rotation cycle result from dynamic environmental factors (e.g., trends in climate change), evolution of stand structure, tree age, and long-term memory of past events (e.g., acclimation). For both studied traits, the dynamics of within-population variances differed among species and populations with no clear pattern. The temporal variations in within-population variances were sometimes important but did not exceed the largest between-population differences of average values. Thus, averaging over temporal intervals, as we did here, provides more robust estimates of within-population variance of growth-related traits. Moreover, stand age had no effect on either trait (mean population values and variances), suggesting that we indeed captured an individual effect independent of cofactors such as tree age or size.

4.2. A growth vigor-sensitivity trade-off within populations facing drought stress

We observed a positive correlation between vigor and sensitivity to drought stress within 17 of 22 populations (77%) in both juvenile and largely mature stands. Vigorous trees showed higher sensitivity to drought stress episodes. Conversely, trees with higher sensitivity showed a higher capacity to benefit from favorable years. These correlations can originate from different and non-mutually exclusive environmental and genetic causes.

The observed positive correlation between vigor and sensitivity could first result from the acclimation of trees to the spatially heterogeneous microenvironmental conditions within stands. In microsites with low available water (e.g., low ESW) and/or high evapotranspiration (e.g., high density of trees, high LAI), individual trees may experience higher drought stress than expected on average and

respond adaptively through shifts in allocation to foliage, sapwood, and roots at the expense of vigor. Adaptive responses include short-term reductions in leaf area through early senescence (Ciais et al., 2005; Bréda et al., 2006), resource-intensive adaptations in hydraulic architecture and wood density induced by longer-term growth (Ruiz Diaz Britez et al., 2014), and lasting global physiological, morphological and architectural changes (e.g., tree height, number and longevity of stems, leaves and roots; Nicotra et al., 2010). Conversely, under favorable microsites (e.g., higher ESW, better fertility), the accumulation of aboveground biomass due to growth may increase the sensitivity to drought events, since these morphological investments in stems and leaves induce substantial maintenance costs in water and carbohydrates during dry periods (McDowell et al., 2011; Cailleret et al., 2019). Changes in the heterogeneity of stand structure (e.g., LAI, tree crown volume, clumping) through forest dynamics and silvicultural interventions are expected to lead to temporal variations in the vigor–sensitivity correlation, as observed. The pronounced spatial heterogeneity often associated with shallow soils could lead to a higher correlation between sensitivity and vigor, as we observed in lower ESW environments (Nourtier et al. 2014).

The vigor–sensitivity correlation could also be of genetic origin, whereby selection for vigor entails a functional cost in terms of sensitivity and *vice versa*, potentially resulting in the coexistence of different genotypes within the population. Stomatal control determines the reduction in assimilation during water deficit periods. Therefore, genotypes characterized by maximum transpiration and assimilation rates under favorable conditions, and thus by high vigor, are expected to show stronger stomatal control during dry episodes, reducing carbon assimilation accordingly (Roussel et al., 2009a,b; Martínez-Vilalta et al., 2012). Vigor can be associated with a larger leaf area, which implies more photosynthesis and thus more growth but also more water loss through evapotranspiration and thus greater sensitivity (Marron et al., 2003). Lower sensitivity can be associated with increased root development, with the allocation of resources to the roots resulting in a substantial cost in terms of aboveground growth (Aranda et al., 2010). Wood density, a trait implicated in resistance to cavitation, is related to slower growth and longer life (Chave et al., 2009). Although universal, this relationship is not systematically found at the intraspecific level (Fajardo et al., 2022). The coexistence of different

adaptive combinations of growth, phenology and anatomy traits, i.e., trait syndromes, was observed in a water-stressed population of *F. sylvatica* (Bontemps et al., 2017). Here, we observed a weaker correlation between vigor and sensitivity in higher extractable soil water environments, i.e., lower drought stress environments, which suggests a low selection pressure on sensitivity leading to the persistence of genotypes *a priori* unfavorable, that is to say not so vigorous but sensitive. The effect of ESW on the correlation between vigor and sensitivity is also consistent with the lack of a significant relationship between drought stress and growth for plots with low stress level. Thus, environmental conditions favoring drought stress, such as low extractable soil water, might be necessary to reveal the trade-off between growth sensitivity and vigor.

4.3. Implications for population adaptation and management under climate change

Forest dynamics tends to progressively lower the social rank of trees with lower growth and then, in particular for shade-intolerant species, to eliminate them through asymmetric competition (Hülsmann et al., 2018). Both vigor and sensitivity are components of tree growth, and we can expect different selection intensities for sensitivity and vigor depending on the local drought regime. When drought is rare or absent, the selection will operate only on vigor, which is likely to indirectly induce the selection of sensitive trees through the trade-off or, at least, to maintain sensitive trees at a dominant social rank. In contrast, the more intense and/or regular the drought events, the greater the selection will operate against sensitivity, which is likely to indirectly select for less vigorous trees. In the context of climate change, we expect such local shifts in drought regimes through increasingly frequent and severe dry conditions. Despite the strong interindividual variations observed, a genetic correlation could restrain the response to selection and contribute to maintaining within-population genetic variation for both sensitivity and vigor (Pujol et al., 2018). Regarding the evolution of forest functions under climate change, selection for lower sensitivity may correlate with selection for reduced growth potential. Depending on the underlying genetic determinism, this is likely to lead to changes in population growth performance over generations.

Forest management modifies the composition, structure, environment, and therefore evolutionary processes of forest tree populations (Jactel et al., 2009; Lefèvre et al., 2014). When

silvicultural operations consist of controlling competition by removing trees on the basis of their phenotype, one issue is that current selection criteria may not necessarily correlate with future adaptedness (Lefèvre, 2012). Indeed, our results suggest that systematically favoring fast-growing trees could be unsafe if water conditions deteriorate because this risks indirectly selecting sensitive trees and, therefore, affects future growth performance. Furthermore, choosing the fastest growing trees among those that remain as seed trees may possibly increase the growth sensitivity in the following generations depending on the underlying genetic basis. When silvicultural practices are used to buffer the intensity and therefore the impact of drought stress (e.g., reduction in stand density and LAI, Giuggiola et al., 2013; Schmitt et al., 2020), attention must be given to avoid over-selection of vigorous and sensitive genotypes and to avoid too much counter-action of acclimation processes. It is expected that the later these practices are applied, i.e., at a mature stand stage, the less the impact on selection for sensitivity will be, since much of the selection will have already taken place before (Lefèvre et al., 2014). One strategy could then be to maintain a significant drought stress level in the juvenile stage to favor adaptation and acclimation before reducing it through thinning or pruning. Ideally, this reflection should address multiple stressors rather than just one, and not just traits associated with growth. In addition, microsite heterogeneity within populations deserves attention in forest management strategies because it provides a variety of conditions with multiple benefits, in terms of resilience of the whole population and in terms of within-population genetic diversity (Scotti et al, 2016; Gauzere et al, 2020).

Only a modeling approach seems to be able to explicitly account for the complexity of the underlying interactions between demography, ecology, management and evolution (Oddou-Muratorio et al., 2020). Such models should consider all demographic performances, i.e., survival and reproduction in addition to growth, and the potential trade-offs between them as well as the underlying genetic basis for questions on a multigenerational scale.

5. Conclusions

We assessed within-population variation and covariation for growth performances, considered as dynamic phenotypic traits. We focused on two growth traits: vigor and sensitivity to drought stress.

The phenotypic variation in vigor and growth sensitivity was considerable in all studied forest tree populations, and we observed a general trade-off between individual tree vigor and sensitivity to drought. The phenotypic variation within populations can be related to better resilience and evolvability, whereas the trade-off represents a potential constraint on adaptation. Overall, the phenotypic variation observed is expected to influence evolutionary trajectory and forest stand dynamics, forest management being impacted by and having an impact on this variation. In particular, selective thinning aimed at favoring fast-growing trees could indirectly: (i) increase population sensitivity to water stress, (ii) harm the process of acclimation, and consequently (iii) affect future growth performance under climate change. Here, management practices supporting the conservation of both slow-growing and fast-growing trees within populations could be considered as a possible strategy to mitigate the negative effects of droughts and increase population resilience.

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3. Vers l'estimation des paramètres génétiques de sensibilité pour la suite de l'étude

En plus d'un formalisme de régime d'impact, cette étude *in situ* apporte de précieuses informations sur la variation phénotypique intra-peuplement des performances de croissance face au stress hydrique. Le fait d'avoir synthétisé les informations sur cinq essences aura aidé à proposer des gammes de variations phénotypiques réalistes. Néanmoins, un défi majeur pour lancer des simulation démo-génétiques consiste à trouver des sources d'information pour estimer les paramètres génétiques (variances additive, héritabilité, etc.) des performances démographiques (Oddou-Muratorio et al., 2020). Les données peuvent provenir d'expériences contrôlées, mais les expériences contrôlées en génétique n'expriment généralement pas l'étendue des conditions environnementales rencontrées en forêt et sont souvent limitées aux arbres juvéniles, tandis que les expériences contrôlées en sylviculture n'explorent souvent pas l'étendue des génotypes. Alternativement, les données peuvent provenir d'approches *in situ* : les paramètres génétiques quantitatifs, tels que l'héritabilité des caractères, peuvent être estimés à partir d'une analyse des covariances individuelles et génétiques entre paires d'individus combinée à des statistiques spatiales (Ritland, 1996). Ces analyses empiriques sortent du cadre de la thèse.

Dans la suite de mon travail, les valeurs des paramètres génétiques de vigueur et sensibilité, ont été estimées à partir des variances phénotypiques observées dans les peuplements du réseau RENECOFOR en supposant une valeur d'héritabilité au sens strict de 0,3 ; ce qui est couramment observé pour ces types de traits quantitatifs (Alberto et al., 2013 ; Depardieu et al., 2020). En outre, la nature générale et multi-espèce du compromis observée entre vigueur et moindre sensibilité ainsi que les évidences bibliographiques de pléiotropies médiées (un gène code pour le trait X et le trait X cause le trait Y) de traits associés à la sensibilité et à la vigueur donnent des preuves solides de son origine au moins partiellement génétique. Néanmoins, la version actuelle du modèle de génétique quantitative de Luberon2 ne permet pas de prendre en charge de telles corrélations génétiques pléiotropiques. Aussi, dans la suite de mes travaux, les simulations à partir de Luberon2 seront exécutées sans corrélation génétique initiale. Je discuterai des possibles biais associés à cette contrainte

méthodologique tout en restant particulièrement attentif quant à l'émergence éventuelle de corrélations qui résulteraient dynamiquement des processus démo-génétiques du modèle.

VII - Evaluation Démo-Génétique des stratégies d'adaptation de la sylviculture du sapin Douglas aux sécheresses

1. Développement de Luberon2 dans le cadre de mes travaux

Pour plus de détails sur les étapes de développement du modèle démo-génétique Luberon2 dans le cadre de mes travaux, des ressources de développement se trouvent en Annexe 2.

1.1. Implémentation du sapin Douglas

L'option technique retenue pour le développement du modèle démo-génétique sapin Douglas a été de récupérer les fonctions de croissance et de mortalité d'un modèle de dynamique forestière sapin Douglas préexistant sur la plateforme Capsis pour les inclure dans le modèle Luberon2. Le modèle de dynamique de peuplements de sapin Douglas préexistant retenu est Gymnos, développé par Gauthier Ligot, Jérôme Perin et al., de l'Université de Liège. Gymnos est un modèle de dynamique forestière individu-centré de pas de temps annuel simulant la dynamique de peuplements équiens de différentes espèces de conifères, y compris le sapin Douglas. Les équations du modèle ont été choisies et ajustées par Jérôme Perin (2013, 2017). Nous avons réalisé l'implémentation de ces équations dans Luberon2 en collaboration avec François De Coligny (UMR AMAP) et Gauthier Ligot sur la plateforme Capsis. Ce travail a demandé une restructuration partielle du modèle Luberon2 dans l'objectif de rendre possible la simulation de peuplements monospécifique de différentes espèces en tenant compte des spécificités propres à chacun des deux modèles de dynamique forestière. Luberon2 est aujourd'hui dans une version fonctionnelle pour le cèdre comme pour le sapin Douglas.

1.2. Implémentation du régime d'impact sécheresse

Luberon2 vise à retranscrire la capacité d'adaptation globale d'un peuplement par une approche dynamique de la sélection au travers de l'impact des perturbations sur les composantes démographiques de la valeur sélective que sont la croissance, la survie et la fécondité. Dans le temps imparti pour ma thèse, j'ai développé le formalisme, l'implémentation

et la calibration de l'impact de la sécheresse sur la croissance, mais il était important d'étendre cet exercice à la survie et à la fécondité.

La rareté des données empiriques sur les relations pression–impacts démographiques, principalement en termes de survie et de reproduction, avait été identifiée comme un défi dans ma démarche. Néanmoins, la dynamique du modèle permet déjà de prendre en charge une partie de ces impacts. En effet, la réduction de croissance impacte mécaniquement la fertilité individuelle, qui est une fonction du DBH et de la taille du houppier des arbres (plus un arbre est gros et plus il produit de gamètes). En outre, une mortalité indirecte liée au stress a été ajoutée à Luberon2. Ici, la probabilité de mourir est liée à l'impact de la perturbation sur la croissance ; le formalisme et la calibration associés s'inspirent du modèle ClimFor (Bugmann, 1996). Cette probabilité de mortalité est donc liée à la sensibilité en termes de croissance, tels que les arbres les plus sensibles ont une probabilité accrue de mourir, ce qui reproduit les mécanismes par lesquels les arbres moins résistants et moins résilients au stress hydrique en termes de croissance affichent un risque de mortalité accrue lors de sécheresses importantes (DeSoto et al., 2020). D'autres impacts directs de la sécheresse sur la survie (par ex. par cavitation) et sur la fertilité mâle ou femelle non liés à la réduction de croissance ne sont actuellement pas pris en compte dans le modèle.

L'implémentation dans Luberon2 des différentes composantes du risque associé à la sécheresse, à savoir l'aléa (fréquence d'occurrence des différentes intensités), les facteurs de sensibilité à l'échelle de l'individu (sensibilité de la croissance au niveau de stress hydrique [génétique et micro-environnement]) et de son peuplement (surface foliaire, réserve utile en eau du sol) ainsi que les relations pression–impact, a été effectuée sous la forme d'un module d'impact démographique sur la croissance.

2. Article 4 (en cours de finalisation). Silviculture as an eco-evolutionary lever for risk management under drought disturbance regime

Le contenu de cette section correspond à un article en cours de finalisation portant sur l'analyse d'un plan de simulation avec Luberon2 qui tire partie du formalisme de régime d'impact sécheresse appliqué au sapin Douglas. Les caractères étudiés sont la vigueur et la sensibilité au stress en termes de croissance. L'objectif ici est de quantifier le rôle des processus évolutifs dans l'atténuation de la vulnérabilité aux sécheresses d'une part, et, d'autre part, à évaluer des stratégies contrastées d'adaptation de la sylviculture aux sécheresses en considérant à la fois les bénéfices d'une réduction du niveau de stress à court terme et les impacts sur l'adaptation génétique sur quelques générations. En tant que premier auteur, j'ai développé le module d'impact sécheresse, conçu et exécuté le plan de simulation, réalisé les analyses, réalisé les figures et rédigé entièrement la première version de l'article.

Les résultats montrent une réponse adaptative rapide en termes de moindre sensibilité face aux impacts répétés des perturbations de type sécheresse sur la croissance et la survie. En même temps, l'augmentation du stress limite la sélection pour la vigueur. Ici, les résultats mettent en évidence un mécanisme de sélection antagoniste susceptible de participer au compromis génétique souvent observé entre vigueur et moindre sensibilité. Les taux d'évolution de vigueur et de sensibilité sont dans une gamme empirique réaliste. Le gain génétique de moindre sensibilité produit une augmentation rapide des performances du peuplement en termes de croissance et de survie face au stress appréciable dès la première génération. En outre, plus le scénario sylvicole est intensif, plus le potentiel évolutif est limité. Les résultats montrent qu'en l'absence de variation génétique, la meilleure stratégie pour favoriser la croissance est de limiter le niveau de stress et donc de s'orienter vers une sylviculture plus intensive. A l'inverse, dès lors qu'il y a de la diversité génétique, c'est-à-dire le cas réaliste, une sylviculture moins intensive, visant à favoriser l'adaptation spontanée, représente la meilleure stratégie. En particulier, le maintien d'un niveau élevé de stress à un stade de peuplement juvénile semble être une stratégie prometteuse pour favoriser l'adaptation et potentiellement l'acclimatation précoce. Les limites d'application de cette stratégie sont discutées.

Silviculture as an eco-evolutionary lever for risk management under drought disturbance regime

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Abstract

In forest ecosystems, a classic adaptation strategy to climate change is to maintain low tree density with frequent thinnings, i.e. more intensive silviculture, which reduces stress levels during droughts with direct benefits on growth and survival. An alternative strategy is to favour the evolutionary potential and maintain the selective pressure in a juvenile stage, with fewer forestry interventions to enhance acclimation and selection. Within the agent-based demo-genetic modelling (DG-ABM) framework, we simulated three successive generations of Douglas-fir grown in pure stands with the Luberon2 model to (i) quantify the potential of natural selection on growth vigour and sensitivity to stress, (ii) understand to what extent genetic diversity and selection are likely to attenuate the vulnerability of tree populations and (iii) assess the influence of management strategies on vulnerability and the underlying eco-evolutionary mechanisms.

We simulated four silvicultural scenarios: a scenario without any thinning to quantify potential for natural selection alone, a trend scenario as a baseline and an intensive scenario as well as a juvenile stress scenario to assess adaptive strategies.

We observed a rapid natural selection response that induced a strong response in stand performances to contrasted drought-like disturbance regimes. Then evolution rate H_0 in vigour and sensitivity varied, in absolute value, between 0.181 and 0.416 SD per generation, which match the usual range of empirical microevolution studies. Here, we highlighted an antagonistic selection mechanism

between selection for vigour and against sensitivity: the relative contribution of vigour to the overall tree growth decreases with increasing stress level and selection by stress competes with selection by competition for the available genetic diversity. In only three generations, dominant diameter was up to 2 times greater and stand biomass production up to 1.6 times greater with genetic diversity than without, while stress-induced mortality rate decreased from 39% to 8%. The more intensive the silvicultural scenario, the more the evolutionary potential was limited. Without genetic variation, the more the silviculture was intensive, the larger the dominant diameter was whereas, conversely, with genetic variation, the more the silviculture was intensive, the smaller the dominant diameter was. Systematically, the more intensive the silviculture, the lower the biomass production. We discuss the mechanisms under these results, the implications for forest management and the use of DG-ABMs as decision support tools to account for eco-evolutionary processes in human interventions.

1. Introduction

Disturbances are important drivers of the dynamics of landscapes and ecosystems and are necessary for the survival and sustainability of many pioneer species and communities (Brawn et al., 2001; Stromberg et al., 2007; Goodale et al., 2012). Terrestrial ecosystems are influenced by disturbances of all kinds, such as droughts, wildfires, frost, storms, landslides, floods, pathogen outbreaks, etc. Although the study of single disturbance events is essential to understand the physiological mechanisms of organisms' responses, understanding the full implication of disturbances in the eco-evolutionary dynamics (i.e. the reciprocal effects that ecology and evolution have on each other Pelletier et al., 2009) requires moving to the scale of the disturbance regime (Banks et al., 2013). A disturbance regime can be defined by a spatio-temporal distribution in terms of intensities, spatial characteristics including area, shape, and discrete or diffuse pattern, and temporal characteristics including duration, frequency, and return interval (White & Jentsch, 2001). Climate change has resulted in many disturbance regimes becoming non-stationary, with an increase in frequency and magnitude (Seidl et al., 2014; 2017). Such alterations in disturbance regimes have direct impacts on the performances of individuals in terms of growth, reproduction and survival, and therefore affect the ecological, demographic and evolutionary processes of populations (Banks et al., 2013). Moreover, they induce a risk of exceeding the ecological resilience of populations, which could lead locally to demographic collapses and extinctions (Reyer et al., 2015; Johnstone et al., 2016; Seidl et al., 2016). In the future, we know that these changes in disturbance regimes will continue, but there are great uncertainties about their magnitude (Dale et al., 2001; Allen et al., 2015). This context confronts us with the limits of our predictive capacity. We must take these limits into account in our socio-ecosystems management choices to develop resilience strategies (Holling, 1973).

In the case of forest ecosystems, management choices and silvicultural practices have multiple effects on the eco-evolutionary dynamics of the forest and represent as many potential levers for reducing the vulnerability of forests to disturbances. A first lever consists in acting directly on the potential impacts of the hazard (Jactel et al., 2009; Moreau et al., 2022). Indeed, the choice of species planted or favoured, the thinning scenarios or the type of regeneration are major drivers of the structure, composition and dynamics of forest stands, which will themselves determine both the magnitude of stress induced by disturbance factors and the susceptibility of the stands, for example, to pathogens (Tainter & Baker 1996), insect pests (Wainhouse, 2005), wind (Quine et al., 1995), fires (Peterson et al., 2005) or drought (Metz et al., 2016). Multiple silvicultural practices interact with each other, potentially in an antagonistic way, hence, ultimately, risk needs to be managed globally and on a local scale. Another lever consists in using silviculture to act dynamically on the trajectory of

adaptedness, resilience and adaptability of tree populations (Lefèvre et al., 2014). Indeed, within stands, the chemical and mechanical treatments, the thinning scenarios or the choice of seed trees will all have effects on the environmental constraints, on the individual genotype composition, and on the population demographic processes. Consequently, whether voluntary or not, any silvicultural practice has multiple consequences on the evolutionary processes. The design of climate change adaptation strategies should, as far as possible, consider all the factors and possible interactions likely to influence their outcomes, in particular the short-term benefits of reducing stress in the current tree population or its long-term effects on genetic adaptation across generations.

In the current context of climate change, a crucial question is the impact of droughts on forests (REF), and the role of forestry in mitigating the effects of droughts on tree survival and growth. Silvicultural interventions such as pruning or thinning directly reduce the leaf area index (LAI) by removing live branches or whole trees (Davi et al., 2008; Forrester et al., 2012), whereas without interventions LAI is likely to increase from juvenile to mature canopy stage (Duncker et al., 2012). LAI determines the water balance of forest soils, since with low LAI, the canopy transpires less and intercepts less rainwater (Bréda et al., 1995; Bréda, 1999). It thus represents a major factor of susceptibility to drought at the stand scale. As a classical strategy to reduce the vulnerability to drought, intensive silviculture scenarios seek to lower the stress level during droughts with visible short-term benefits on tree growth and survival (Sohn et al., 2016; Schmitt et al., 2020, Gavinet et al., 2020; Moreau et al., 2022). This strategy focuses on the short-term benefits, while the evolutionary processes and genetic impacts are largely ignored or considered only qualitatively (Legay et al., 2015). However, this strategy also has potential long-term effects on two adaptive processes: at individual tree level, a decrease in stress exposure reduces acclimation and, at population level, a lower stress level reduces the selection pressure for resistant individuals which could lead to a genetically less adapted mature stand while older and larger trees are more at risk (increased sensitivity to droughts [Bennett et al., 2015]). In addition, the thinnings, especially when early, intense and systematic, could directly limit selection differential and adaptive potential by removing genotypes before any selection takes hold (Lefèvre et al., 2014). These trade-offs between short-term effects of further thinning to reduce stress during droughts and long-term impacts on acclimation and natural selection are usually not considered in the effort to adapt forest management to the alteration of drought regimes. Our main hypothesis is that an alternative strategy, avoiding early interventions to maintain stress in the juvenile stage while reducing density in a later stage could favour acclimation and preserve diversity for the selection of resistant trees, could lead to a genetically better adapted mature stand.

This study aims to investigate the multiple effects of interactions between management practices and drought on the demo-genetic dynamics of forest stands. Predicting short term, i.e. over a forestry cycle, and long term, i.e. across several regeneration steps, evolutionary consequences of different management strategies is a challenge, particularly for long-lived species like trees. The demo-genetic agent-based modelling framework (DG-ABM) is appropriate to develop simulation approaches that account for interactions between human interventions and evolutionary processes (Oddou-Muratorio et al., 2020; Lamarins et al., 2022). Following this approach, we developed a forest dynamics model with heritable trait variation, named *Luberon2*, to simulate the joint effects of natural evolutionary processes including stochastic disturbances and explicit eco-evolutionary feedbacks, genetic diversity and silviculture in monospecific stands (Godineau, Fririon et al., submitted⁸). In this demo-genetic model, natural selection is dynamically driven by individual tree growth in relation with survival and mating success: a bigger tree has a better chance to survive under competition and to contribute to the reproduction due to higher fecundity. It is possible to simulate neutral or non-neutral human interventions, i.e. thinning according to the size of the trees (hereafter, viability selection by silviculture). In *Luberon2*, individual tree growth (and consecutive survival and reproduction) is driven by site fertility, stand age, local competition and individual genetic value for growth vigour.

In this work, we used *Luberon2* to simulate the impacts of droughts on growth, reproduction, survival and genetic diversity of monospecific Douglas-fir stands, on an ecological time scale, i.e. over a few generations. Therefore, we integrated a drought-like disturbance regime in the model, where drought stress level affects the annual growth, also potentially leading to mortality above a threshold of growth reduction (hereafter, viability selection by stress). To account for LAI as a dynamic susceptibility factor, we integrated the drought hazard in the form of a probability distribution of the stress level modulated by the LAI. This work had three main objectives. First, we sought to identify and quantify the evolutionary mechanisms involved in the adaptive response to an environment combining both intra-specific competition and drought-like disturbance. To this end, we quantified the genetic gain in terms of growth vigour and sensitivity through natural selection, depending on disturbance regime and initial genetic diversity. Second, we studied how genetic diversity and selection are likely to attenuate the vulnerability of tree populations. To this end, we quantified the population growth and stand productivity, depending on disturbance regime and initial genetic diversity (here, we considered the case of an initial plantation followed by natural regeneration, i.e. initial genetic diversity considered as a management choice). Third, we explored how forest management could control the vulnerability of populations through driving the evolutionary mechanisms. To this end, we quantified the impacts of

⁸ Supposé soumis lorsque le présent article sera lui-même soumis.

current and innovative silvicultural routes on adaptedness, productivity and population growth and comparatively assessed the risks, costs and benefits associated with various silviculture strategies, i.e. intensive silviculture vs maintaining juvenile stress, depending on disturbance regime and initial genetic diversity.

2. Material and methods

2.1. Overall description of Luberon2

Luberon2 results from the coupling of forest dynamics models with a robust quantitative genetic model. The current version runs either for cedar (*Cedrus atlantica* (Endl.) Manetti ex Carrière) or for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). For a complete description of Luberon2, refer to Godineau, Fririon et al., (submitted). The model is developed on the Capsis modelling platform, available at <https://capsis.cirad.fr/capsis/download>. The demographic components of the model include growth and mortality caused by competition between trees (self-thinning), initially calibrated for Douglas fir on empirical data by Perin et al. (2013; 2017). Self-thinning preferentially eliminates small trees, i.e. the less competitive ones. For the regeneration process, we simulated the number of cones per tree as for *Cedrus atlantica* (Godineau, Fririon et al, submitted) with the expected number of seeds per cone for Douglas fir (REF). Luberon2 relies on distance independant tree models and simulates regeneration in even-aged by patches stand structure. So, the whole scene is split into uniform and independent growth units (15 m × 15 m by default) where demographic processes occur, except pollen and seed dispersal operating at the scene scale composed of 441 growth units. The consequences of the patch structure on growth and demographic predictions are further discussed in Godineau, Fririon et al (submitted).

As a DG-ABM model, the annual evolution loop of Luberon2 corresponds to an eco-evolutionary feedback loop where the quantitative genetic model determines the variance in performances of individual trees from genetic diversity, while the forest dynamics model determines stand structure based on individual performances in terms of growth, reproduction, and survival. The structure of the stand is itself a condition of the environment driving the selection pressure, i.e. competition and water stress that are both density dependent. Systematic or selective silvicultural interventions can modify the stand composition and structure Genetic evolution results mechanically from the demographic processes and from silvicultural interventions, without any prescribed function between the performance traits and fitness.

Here, we considered two evolvable traits, growth vigour and sensitivity.

2.2. Modelling drought stress level and definition of disturbance regimes

Based on the even-aged forest dynamics model *Gymnos* calibrated for Douglas-fir, each year and for each tree of each growth unit, diameter increment is computed according to the initial tree circumference and the basal area and dominant height of the growth unit (Perin et al., 2013; 2017). We added a new disturbance model in *Luberon2* by simulating a stochastic stationary drought-like disturbance regime, which reduces the annual increment in diameter predicted by the growth model, according to the formalism proposed in a previous publication (Fririon et al., 2023).

Each year n , the climatic hazard intensity for the whole scene (I_n) is drawn in a Uniform distribution in the interval $[0,1[$. Within each growth unit, the quantile function of the Gamma distribution returns the *StressLevel* corresponding to I_n . Thus, in a given year, I_n is common to the whole scene but the *stressLevel* varies among the growth units according to LAI.

Within each growth unit, the distribution of the stress level (*StressLevel*) is modelled as a Gamma distribution, $\Gamma(shape, scale)$, defined with six parameters depending on the current LAI:

$$shape = a_{shape} \times LAI^{b_{shape}} + c_{shape} \quad (equation 1),$$

$$scale = a_{scale} \times LAI^{b_{scale}} + c_{scale} \quad (equation 2),$$

where a_{shape} , b_{shape} , c_{shape} , a_{scale} , b_{scale} and c_{scale} are six parameters defining the Gamma distribution.

The computation of the leaf area index (LAI), required for the growth reduction disturbance process, was added to the original growth model. An allometric relationship calibrated for Douglas-fir (Smith, 1993) has been implemented to estimate the LAI in each growth unit from individual tree diameters at breast height (DBH) considering stand density on tree crown morphology (on the individual leaf area), as follows:

$$LAI_p = \frac{1}{Area_p} \times \sum_i LA_i \quad (equation 3),$$

where the leaf area index of a growth unit p (LAI_p) is the sum of the leaf areas of its individual trees i (LA_i) relatively to the area of the growth unit ($Area_p$), with:

$$LA_i = 0.4781 \times DBH_i^{1.8659} \times \exp(-0.0829 \times RD_p), \quad \text{with } RD_p = \frac{Gha_p}{Dg_p^b} \quad (equation 4),$$

where the leaf area of individual i , LA_i , is obtained by allometry from its DBH_i , and the Curtis' relative density of the growth unit p , RD_p (Curtis, 1982); the Curtis' relative density is obtained from the basal area, Gha_p , and the root mean square diameter, Dg_p , of the growth unit and a species specific parameter, $b = 0.5$ for Douglas-fir.

We carried out the calibration of three *stressLevel* Gamma distributions to cover the range of water stress regimes observed over the European use range of Douglas-fir. This work is briefly described below and in more detail in Appendix A. In a first step, we quantified drought stress levels over the realised European range of Douglas-fir. To do so, we used the aggregation of European pedoclimatic data by Petit-Cailleux et al. (2021) and ran the process-based ecophysiological model CASTANEA (Dufrêne et al., 2005; Davi & Cailleret 2017) from 1979 to 2008 on the 698 raster cells (resolution of 0.5° per 0.5°) containing at least one Douglas-fir stand (Mauri et al. 2017). Based on pedoclimatic data, species-specific ecophysiological data and LAI value, CASTANEA simulate the annual soil water balance and integrates it in the form of an annual water stress level indicator (*StressLevel*) computed as a Palmer index measured in MPa (Palmer, 1965; Fririon et al., 2023). For each raster cell, we ran nine simulations by varying the LAI value between 2 and 10, which corresponds to the LAI range generally observed in naturally regenerating Douglas-fir stands (Smith et al. 1993). In a second step, we analysed the time series of *stressLevel* thus obtained per raster cell and per LAI value in the form of Gamma distributions, $\Gamma(shape, scale)$. As a sum of water potential, the *stressLevel* is systematically negative. Constrained by the Gamma distribution calibration algorithms, in this article, we use the absolute values of *stressLevel*, which also goes in the most logical way: a high positive *stressLevel* value corresponds to high stress. We selected three *stressLevel* regimes based on average *stressLevel* and under condition of compatibility with the formalism of Luberon2 (eq. 1,2). The three *stressLevel* regimes are a zero-stress regime (disturbance unactivated), a medium stress regime, affecting growth but with little impact on survival according to pre-analyses with Luberon2, and a intense stress regime, strongly affecting both growth and survival (punctually, the annual mortality rate could reach 30%). For the medium and intense stress regimes, we fitted the parameters a_{shape} , b_{shape} , c_{shape} , a_{scale} , b_{scale} and c_{scale} by nonlinear regression to obtain the simulated *stressLevel* Gamma distributions modulated by the LAI over the European use range of Douglas-fir.

2.3. Evolvable traits: growth vigour and sensitivity

2.3.1. Individual genotypes

Genetic variation of each trait is modelled through individual explicit genotypes at 20 diallelic QTL following an additive inheritance model. Each diallelic QTL is characterised by an allelic effect, one allele providing the positive value of this effect and the other one the negative value. For each

quantitative trait, the genotypic value of an individual is the sum of the effects of its alleles over the QTL controlling the trait and, therefore, a full heterozygous individual has a null genotypic value. The additive genetic variance of each trait in the population is the sum of the contributions of its QTL (l):

$$VA = \sum (1 + Fl) 8p_l q_l a_l^2 \quad (\text{equation 5}),$$

where Fl is the fixation index, p_l and q_l the allelic frequencies, and a_l the allelic effect of the QTL (thus the allelic substitution effect is $2a_l$). Individual genotypes in the initial stand were simulated using the simulation tool Metatrom (Godineau, Fririon et al., submitted), a heuristic algorithm to fit population target values and quantitative genetic parameters, i.e. additive variance and number of QTL. In Godineau, Fririon et al., (submitted), we observed that different sets of QTL allelic effects and frequencies leading to the same target variance and the same architecture may result in different evolutionary rates. The effect of the initial set of genotypes fades with the increase in the number of QTL. Here with 20 QTL, we can expect a weak effect. Therefore, here we used a single set of initial genotypes. The individual genotypes of the new seedlings directly result from random association of gametes from both parents which are retrieved from individual male and female fecundity and seed and pollen dispersal functions.

The individual phenotypic values are obtained by adding to the individual genetic value an individual fixed environmental value drawn in a normal distribution with mean 0. The environmental variance is obtained from the initial genetic variance and heritability input parameters. The management of genetic information, i.e. the effect of the genotype on the phenotype and the hereditary transmission of genes, is controlled through the Genetics library of Capsis (Dreyfus et al., 2004; Seynave & Pichot, 2004).

2.3.2. Initial genetic diversity of growth vigour and sensitivity

The first trait under genetic control and inherited in Luberon2 is growth vigour. The vigour of an individual is defined as the deviation to the individual growth model. When there is no stress, it is the only trait involved in the growth performance of an individual, which can then achieve its potential diameter increment ($dDnoStress_i$):

$$dDnoStress_i = dDexpected_i + Ind_vigour_i \quad (\text{equation 6}),$$

where $dDexpected_i$ is the predicted diameter increment from the growth model for an individual i and P_vigour_i is the individual phenotypic deviation to the growth model.

The second trait under genetic control in Luberon2 is growth sensitivity to stress. For a given individual, it is defined as the relative loss of potential growth per unit of stress. The effective sensitivity of an individual has two components: a stand value common to all individuals used to scale the growth phenotypic plasticity model and the individual phenotypic deviation from this stand value which can therefore be positive or negative. The impact of stress on growth is computed as:

$$dDstress_i = dDnoStress_i(1 - StressLevel \times (stand_sensitivity + Ind_sensitivity_i)) \quad (equation\ 7),$$

where $dDstress_i$ is the diameter growth after stress impact, $dDnoStress_i$ the potential diameter increment (without stress), $stand_sensitivity$ the stand mean sensitivity, and $P_sensitivity_i$ the individual phenotypic deviation to the stand mean value. In order to avoid negative effective sensitivity values (better growth under stress) that may occur for trees with a highly negative phenotypic deviation from the stand value, the overall individual sensitivity is constrained to be above a minimum value of 10% of the stand value.

Depending on the disturbance regime, the most vigorous and/or the least sensitive trees grow best. The smallest trees are eliminated by self-thinning, i.e. viability selection. Each fertile tree in the scene contributes to the pool of gametes according to its size: bigger trees produce more gametes. Thus, individual fertility and relative contributions to the next generation, i.e. fecundity selection, are also affected by vigour, sensitivity and disturbance regime. In addition, two consecutive years of absolute growth less than 0.03 cm, or a 90% reduction in growth potential by stress level is likely to result in tree death with a probability of 36.8%; this formalism and associated calibration being inspired from the ClimFor model (Bugmann, 1996). This reproduces the mechanisms by which trees that are less resistant and resilient to water stress in terms of growth are at increased risk of drought-induced mortality (DeSoto et al., 2020).

A population is genetically characterised by its mean genetic value (which is also the mean phenotypic value) and its genetic variances in growth vigour and sensitivity. The initial mean genotypic value of the vigour is arbitrarily set to 0, as a reference, which means that at initialization the individual genotypic values, and hence the phenotypic values, are centred on the growth model. The initial value of these genetic parameters was estimated based on the study of within-population inter-individual variation in vigour and sensitivity in five species of the RENECOFOR network, including Douglas-fir (Fririon et al., 2023). As a reference, the initial mean stand sensitivity was set to 0.002 MPa^{-1} , corresponding to the average of the observed phenotypic values within Douglas-fir stands. For both variable traits, we retained three levels of initial genetic variances : (i) a zero variance; (ii) a reference variance of $8.0 \times 10^{-3}\text{ cm}^2$ for vigour and $5.1 \times 10^{-7}\text{ MPa}^{-2}$ for sensitivity based on the mean within-

population phenotypic variances observed in Douglas-fir stands assuming narrow sense heritability $h^2 = 0.3$ for both traits as classically observed for these types of quantitative traits (Alberto et al., 2013; Depardieu et al., 2020); and (iii) a high variance of $1.60 \times 10^{-2} \text{ cm}^2$ for vigour and $1.02 \times 10^{-6} \text{ MPa}^{-2}$ for sensitivity corresponding to twice the reference variance.

2.4. Description of the silvicultural scenarios

In this study, we simulated the particular case of an initial plantation subsequently regenerated with natural regeneration. This is not only a theoretical situation: old Douglas-fir forests often show favourable conditions for natural regeneration in Europe (Petit & Claessens, 2013). The first silvicultural cycle begins with 1200 trees per hectare (classic plantation density of Douglas-fir) in 2015 and the trees are 15 years old (Figure 1a); the next two cycles begin with around 2700 naturally regenerated trees per hectare (Figure 1a). A complete silvicultural cycle integrates up to 4 thinnings depending on the silvicultural scenario considered, followed by a seeding cut leaving 100 seed trees per hectare when the stand reaches 50 years. Following the seeding cut, a three-year regeneration phase is initiated. At the end of the regeneration phase and of the forestry cycle, the seed trees are harvested, leaving only the new seedlings. Because it is outside the domain of validity of the model, the seedlings can not be recruited by the growth model before a recruitment age of 15 years for Douglas-fir. As long as the seedlings have not reached the recruitment age, i.e. the pre-recruitment stage, no process of any kind affects them. At the start of recruitment, the age of the seedlings accumulated over the three years of regeneration is fixed at a single value since the growth model is calibrated for even-aged stands and the seedling size is randomly assigned independently of individual genotype: we assume that the effect of genotype is negligible before recruitment age. Each simulation includes three successive silvicultural cycles repeating the same silvicultural scenario, which corresponds to four generations, the last one remaining at the pre-recruitment stage. To allow for comparison, we constrained all scenarios described below to a 50-years cycle with 100 seed trees per hectare left for regeneration. We simulated each scenario over three silvicultural cycles, i.e. 150 years in total, which is consistent with the planning horizon for forest managers and with the long-term assessment of adaptive management for geneticists (Oddou-Muratorio et al., 2020).

We simulated an ***unthinned scenario***, as a reference scenario, with only one random cut at 50 years to obtain the standard seed tree density and final harvest for comparability with other scenarios. As a baseline thinned scenario, we simulated the so-called ***trend scenario*** as proposed for Douglas-fir by the French webservice Forêts-21 for the strategic management of production forests (Aluome et al., 2019). It consists of four thinnings. In addition, we simulated two contrasted original thinned scenarios: (i) the ***intensive scenario***, with earlier and overall more intense thinnings, and (ii) the ***juvenile stress***

scenario, devoid of the first thinning and delayed second thinning by two years to give more weight to natural selection. Within each silvicultural cycle, the LAI increases with stand development and is reduced at each intervention by reducing tree density (*Nha*) (Figure 1b). We designed the intensive scenario to keep LAI always lower than that of the trend scenario while remaining within a plausible *Nha* range (Figure 1a, b). The juvenile stress scenario maintains a LAI identical to the unthinned scenario until the thinning at age 22, then close to the trend scenario (Figure 1b). Each silvicultural scenario was simulated with selective thinnings from below, i.e. preferentially cutting the smallest trees, except for the first thinning carried out randomly, which better mimics the usual practices (Perin et al., 2016). In all cases, the seeding cut was carried out randomly. The number of crop trees, i.e. the number of trees after the last thinning, is the same for each scenario. The four silvicultural scenarios are described in Table 1.

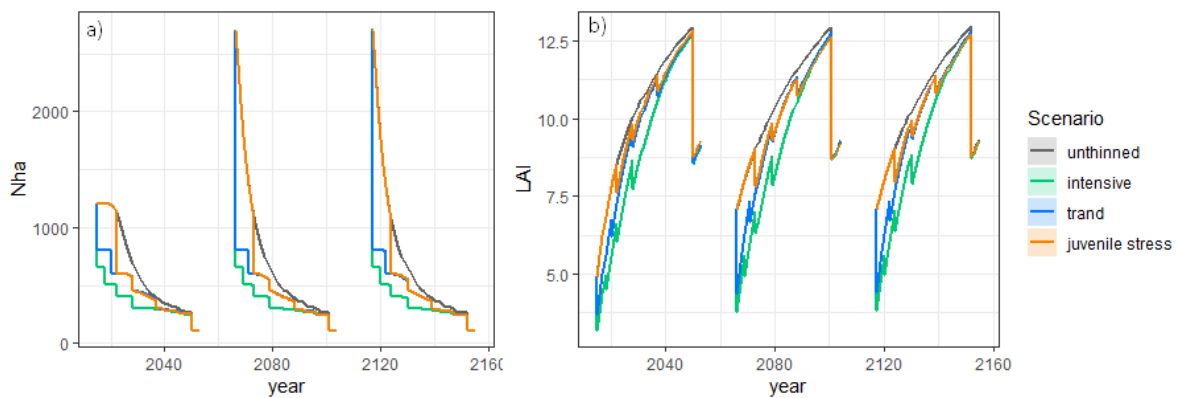


Figure 1. Characterization of the four silvicultural scenarios by the dynamics of the number of trees per hectare (*Nha*) (a) and leaf area index (*LAI*) (b) during three silvicultural cycles with unactivated disturbance and zero genetic variance. The four scenarios are represented by the colours: grey for the unthinned scenario, green for the trend, blue for the intensive and orange for the juvenile stress. The pre-recruitment period is deliberately absent because it constitutes a modelling artefact.

Table 1. Description of the intervention regime of the four silvicultural scenarios, i.e. unthinned, trend, intensive and juvenile stress scenarios. For each intervention of each scenario (thinnings and seeding cut), the age of the stand that triggers the intervention is indicated with the target in terms of number of trees per hectare (*Nha*) in brackets.

Scenario	Thinning 1 (random)	Thinning 2 (from below)	Thinning 3 (from below)	Thinning 4 (from below)	Seeding cut (random)	Final harvest
<i>Unthinned</i>	-	-	-	-	50 ans (100)	53 ans (0)
<i>Trend</i>	15 ans (800)	20 ans (600)	28 ans (450)	37 ans (300)	50 ans (100)	53 ans (0)
<i>Intensive</i>	15 ans (650)	18 ans (500)	22 ans (400)	28 ans (300)	50 ans (100)	53 ans (0)
<i>Juvenile stress</i>	-	22 ans (600)	28 ans (450)	37 ans (300)	50 ans (100)	53 ans (0)

2.5. Simulation plan

The initial scene of all our simulations has an area of 9.9225 hectares divided into 441 growth units of 225 m². The environment is homogeneous with a site index of 40 m at 50 years, which corresponds to a high fertility value for Douglas-fir. The initial stand has a total number of 11,907 individual trees, corresponding to $N_{ha} = 1200$ trees per hectare.

The simulation plan has a total of 36 modalities corresponding to a complete factorial design with four silvicultural scenarios, three disturbance regimes and three levels of genetic variance (Table 2). We performed 10 replicates of each modality to account for stochasticity in disturbance events (e.g. annual stress level), genetic and demographic processes (e.g. reproduction, recombination, self-thinning), as well as silvicultural interventions.

Table 2. Summary of the hierarchical simulation plan crossing four silvicultural scenarios, three drought-like disturbance regimes and three initial genetic variances, with 10 repetitions per modality.

Factor	Number of levels	Description
<i>Silvicultural scenarios</i>	4	Four silvicultural scenarios contrasted in terms of anthropogenic pressure: an unthinned scenario, a baseline silvicultural scenario so-called trend scenario and two original scenarios, i.e. the intensive scenario and the juvenile stress scenario
<i>Disturbance regimes</i>	3	Three stationary stress regimes: a zero-stress regime (unactivated), a medium stress regime, affecting growth but very little survival and an intense stress regime, strongly affecting growth and survival
<i>Initial genetic variances</i>	3	Three initial genetic variances: a zero variance, a reference variance corresponding to an empirical estimation and a high variance corresponding to twice the variance reference.
<i>replicates</i>	10	Ten replicates to consider stochasticity in the processes of the model.

2.6. Analysis of simulation outputs

Luberon2 simulates different output variables (i.e. individual tree characteristics, stand level variables, growth unit level variables) allowing to analyse and compare different simulated scenarios with regard to dendrometric, demographic and genetic variables. In this study, we were particularly interested in comparing genetic gain in terms of growth vigour and lower growth sensitivity, productivity and population growth between modalities. We focused on a limited number of output variables: the *N_{ha}* and the *LAI* to characterise the different silvicultural scenarios; the *StressLevel* to characterise the impact of silvicultural scenarios on disturbance; the population mean genetic value of growth vigour and sensitivity to quantify genetic gains; the dominant diameter and basal area production to quantify stand productivity; the self-thinning and stress-induced mortality rates computed per silvicultural cycle,

to characterise the demographic dynamics and the viability selection pressure. The output variables used in this study are described in Table 3. All these variables are computed by iteration on the trees from their individual characteristics. For a complete description of the output variables of Luberon2, refer to Godineau, Fririon et al. (submitted).

Table 3. Description of the luberon2 output variables analysed for this study.

Output variable	Code	Unit	Description
<i>Number of trees per hectare</i>	Nha	-	The number of live individual trees per hectare
<i>Leaf area index</i>	LAI	-	Dimensionless quantity that characterises forest cover. It is defined as leaf area per unit ground surface area.
<i>Population mean genetic value in sensitivity</i>	$\mu G.Sen_{si}$	MPa^{-1}	The population mean genetic value in sensitivity. The initial value is 0.002 then evolutionary processes, e.g. genetic selection and drift, cause the value to evolve.
<i>Population mean genetic value in vigour</i>	$\mu G.Vig$	$cm \cdot year^{-1}$	The population mean genetic value in vigour. The initial value is 0, then evolutionary processes, e.g. genetic selection and drift, cause the value to evolve.
<i>Dominant diameter</i>	dDom	cm	The mean diameter of the 100 biggest trees per hectare
<i>Basal area production</i>	BAprod	m^2/ha	The basal area, i.e. the sum of all cross-sectional areas measured at 1.3 m, of all harvested trees from the first thinning to the final cut.
<i>Competition-induced mortality rate</i>	CIMR	-	Cumulative number of deaths by self-thinning related to the number of initial trees in a single silvicultural cycle
<i>Stress-induced mortality rate</i>	SIMR	-	Cumulative number of deaths by stress impact related to the number of initial trees in a single silvicultural cycle

Luberon2 allows the export of the simulated data for external analysis. We carried out these analyses with R version 3.6.2 (R Development Core Team, 2019). We performed two types of analysis: a dynamic analysis of annual changes for each output variable of interest to better understand the mechanisms and evaluate their evolutionary kinetics in different silviculture scenarios (intra-generation and between generations), and a global comparison between the silvicultural scenarios after four generations of evolution.

We quantified the evolutionary rate of vigour and sensitivity using the H_0 index (Gingerich 1993; 2009), which represents the overall evolution of a trait in unit of phenotypic standard deviations per generation:

$$H_0 = (zdiff_i / \sqrt{zvar.w_i}) / n.gen \quad (\text{equation 8}),$$

where $zdiff_i$ is the observed change in the population mean phenotypic value in the considered trait in a temporal interval i , $zvar.w_i$ is the pooled intra-population phenotypic variance of the considered trait sampled at the beginning and at the end of the temporal interval i and $n.gen$ is the number of generations. The temporal interval i that we used is defined by the beginning of the first silvicultural cycle and the end of the third, corresponding to three complete generations.

3. Results

3.1. Impact of disturbances and genetic diversity on demo-genetic dynamics (unthinned scenario)

Without disturbance and without genetic variability, self-thinning was the only intra-generational source of mortality (Figure 2). Most self-thinning occurred at the beginning of the silvicultural cycle (Figure 2a). Self-thinning increased in the last cycle as compared to the first one because of the higher initial number of trees (Figure 2a, c). With disturbances, the number, growth and therefore the size of the trees were impacted, which finally resulted in reduced competition-induced mortality rate (CIMR) (Figure 2a). Furthermore, intense stress level induced another type of mortality, the stress-induced mortality rate (SIMR), which interacted with competition-induced mortality, such that stress-induced mortality strongly reduced self-thinning, but not enough to make it disappear in our simulations (Figure 2a). Thus, counterintuitively, the overall mortality was reduced with drought-like disturbance because the reduction of CIMR exceeded SIMR in our situation (Figure 2c).

The presence of genetic variation for growth vigour and sensitivity changed the mortality processes. Without genetic diversity, stress-induced mortality occurred randomly throughout stand development, whereas with genetic diversity the maladapted genotypes (the most sensitive) were rapidly eliminated at the beginning of each silvicultural cycle leading to a progressive reduction of SIMR within each cycle (Figure 2b).

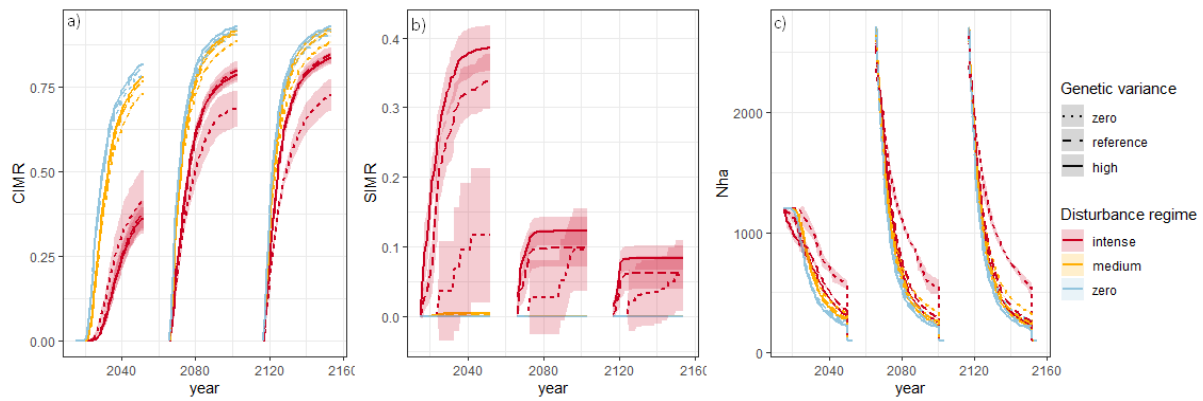


Figure 2. Annual demographic dynamics of the unthinned scenario during three silvicultural cycles as a function of the initial genetic variance and the disturbance regime: the competition-induced mortality rate (CIMR) per silvicultural cycle (a), the stress-induced mortality rate (SIMR) per silvicultural cycle (b) and the number of trees per hectare (Nha) (c). The three disturbance regimes are represented by colours and the three genetic variances by line types, as indicated in the legend. The shaded area represents the 95% confidence interval among the 10 replicates. The pre-recruitment period is deliberately not represented because it constitutes a modelling artefact.

Over the three cycles, without disturbance, the average evolutionary rate H_0 was 0.002 sd per generation for sensitivity and 0.356 for vigour for the reference genetic variance. For the high genetic variance, these evolutionary rates were -0.005 and 0.416 , respectively. With the medium disturbance regime, H_0 was -0.240 sd per generation for sensitivity and 0.269 for vigour for the reference genetic variance; -0.238 SD and 0.320 , respectively, for the high genetic variance. With the intense disturbance regime, H_0 in sensitivity is -0.322 SD per generation (Resp. 0.181 for vigour) for the reference genetic variance and -0.298 SD per generation (Resp. 0.259 for vigour) for the high genetic variance. Overall, most of the genetic evolution of sensitivity and vigour occurs at the beginning of the silvicultural cycle and then slows down (Figure 3ab). Annual changes of mean population genetic value shed light on the multiple mechanisms of selection. As previously mentioned, viability selection by drought stress (selective SIMR) drove the early purge of sensitive genotypes. It led to a rapid decline in mean sensitivity in the first generation (Figure 3a). before any self-thinning, but its relative importance rapidly decreased from one generation to the next: as a feed-back, genetic gain in lower sensitivity reduced the genetic purge (Figure 2b; Figure 3a). Competition-related viability selection (selective CIMR) also drove the evolution of both vigour and sensitivity (Figure 3). Potentially, at each reproduction phase, fecundity selection may operate when more vigorous and/or less sensitive genotypes contribute more due to their bigger size: this mechanism acts in the same direction as viability selection. Simultaneously, each reproduction phase also creates new genotypes and restores the genetic variance: this mechanism counteracts the effect of viability selection on the genetic mean. In our simulations, the second mechanism was slightly predominant and each regeneration phase induced a moderate regression of previous viability selection effects (Figure 3). As expected, higher genetic variance resulted in increased

genetic gain (Figure 3). Selection for vigour and against sensitivity overall increased stand growth performance whatever the disturbance regime and stress. Therefore, as an eco-evolutionary feedback, competition-related mortality was higher with genetic variation than without (Figure 2).

The disturbance regime had opposite effects on the selection processes on vigour or sensitivity (Figure 3). Indeed, the intensity of viability and fecundity selection for vigour and against sensitivity depends on the relative contribution of both traits to overall tree growth because the stronger and/or more frequent the stress, the more tree size depends on sensitivity and the less it depends on vigour. Furthermore, overall mortality and thus selection intensities were lower with disturbance. This resulted in a lower genetic gain in vigour but higher genetic gain in sensitivity with disturbance than without.

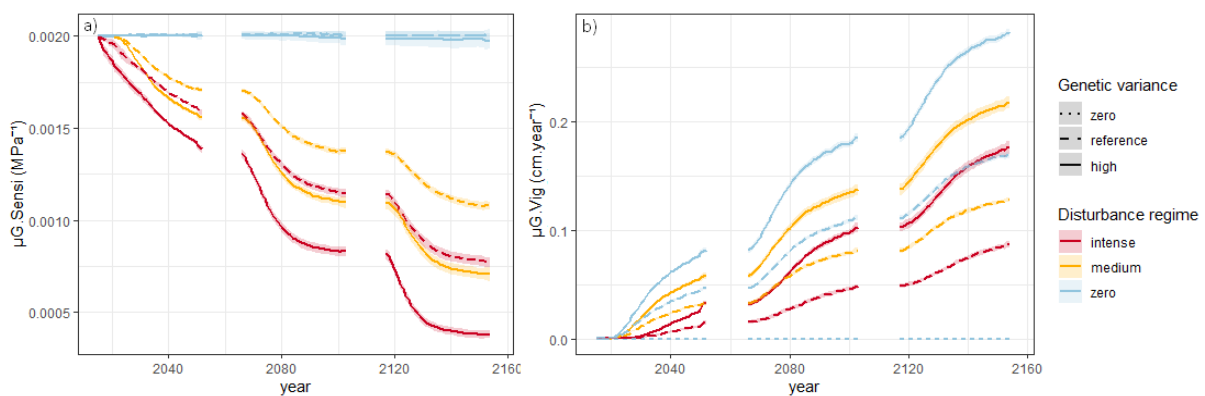


Figure 3. Annual dynamics of the population mean genetic values in growth sensitivity (a) and vigour (b) for the unthinned scenario during three silvicultural cycles as a function of the initial genetic variance and the disturbance regime. The three disturbance regimes are represented by colours and the three genetic variances by line types, as indicated in the legend. The shaded area represents the 95% confidence interval among the 10 replicates. The pre-recruitment period is deliberately not represented because it constitutes a modelling artefact. Without disturbance, there is no selection on sensitivity, minor changes are only driven by genetic drift.

The disturbance regime and the genetic diversity had an impact on annual stand growth performance (Figure 4). This joint impact potentially results from eco-evolutionary feedback because competition has twinned antagonistic effects of inducing a genetic gain on growth-related traits, vigour and/or sensitivity, while reducing the expression of this genetic potential in stand growth performance. Without disturbance, vigour was the only variable trait impacting stand growth performance, and higher genetic variance resulted in higher stand performance (Figure 4). Compared to the modality without genetic variation, the dominant diameter is 19% (resp. 8% for the basal area production) greater with the reference genetic variance and 31% (resp. 13%) greater with the high variance at the end of the third cycle. With disturbance, vigour and sensitivity were both impacting stand growth performance and, in this case, there was an interaction effect between the selection processes on both traits: the more intense disturbances, the higher the beneficial impact of genetic variance on stand growth

performance (Figure 4). With the medium disturbance regime, the dominant diameter is 31% (resp. 13%) greater with the reference genetic variance and 44% (resp. 19%) greater with the high variance at the end of the third cycle. Finally, with the intense disturbance regime, the dominant diameter is 79% (resp. 47%) greater with the reference genetic variance and 97% (resp. 58%) greater with the high variance at the end of the third silvicultural cycle. Since the gain in vigour is reduced by a factor 1.3 with medium disturbance regime and by a factor 1.8 with intense disturbance regime (Figure 3), this rapid recovery in stand growth performance can only be explained by decreased sensitivity.

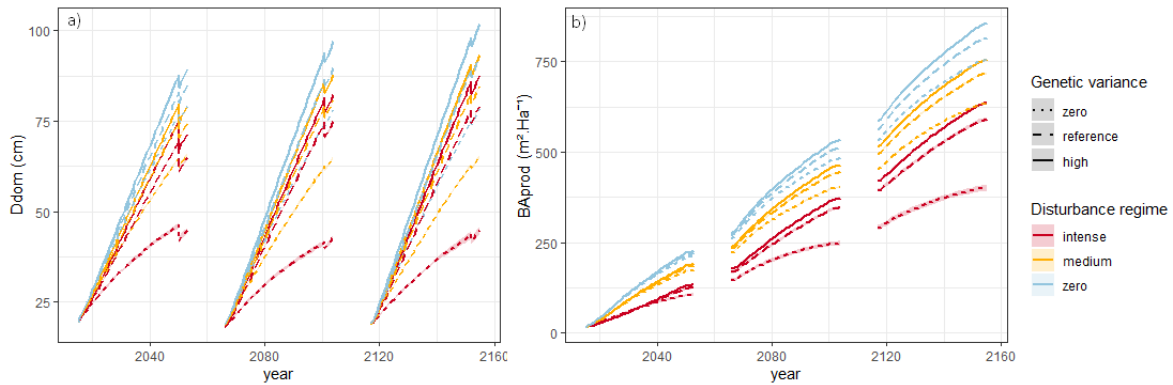


Figure 4. Annual stand growth performance in dominant diameter (a) and basal area production (b) for the unthinned scenario during three silvicultural cycles as a function of the initial genetic variance and the disturbance regime. The three disturbance regimes are represented by colours and the three genetic variances by line types, as indicated in the legend. The shaded area represents the 95% confidence interval among the 10 replicates. The pre-recruitment period is deliberately represented because it constitutes a modelling artefact. The small drop in dominant diameter at the end of each cycle corresponds to the seeding cut: this random intervention is likely to remove the largest tree, among others.

3.2. Impact of silvicultural scenarios on demo-genetic dynamics

Each intervention is an additional selective mortality event that interferes with the natural processes described above.

Without disturbance, we observed a decrease in competition-induced mortality (CIMR) in the intensive, trend and juvenile stress scenarios compared to the unthinned scenario (Supp. Figure B1). The first systematic (i.e. random) thinning of the intensive scenario, and to a lesser extent the trend scenario, removed many trees which thus escaped selection. The absence of the first systematic thinning in the juvenile stress scenario maintained the selection processes equivalent as in the unthinned scenario until the thinning at age 22 (Supp. Figure B1). Trees subsequently thinned in the trend, intensive and juvenile stress scenarios were subject to viability selection by silviculture.

With disturbance, we observed a decrease in both stress-induced mortality (SIMR) and competition-induced mortality (CIMR) (Figure 5; Supp. Figure B2). Increasing thinning intensity relaxed

the two natural mechanisms of mortality. Within each silvicultural cycle, the stress level increased during stand development and was reduced by each intervention (Figure 5c). Among silvicultural scenarios, the stress level regimes were consistent with the variations in LAI (Figure 1b). Thus, the average stress level over the entire silvicultural cycle and the occurrence of high stress events were the highest with the unthinned scenario (average *stressLevel* of 261 Mpa with intense disturbance regime and of 92 Mpa with medium disturbance regime), followed by the juvenile stress scenario in particular before the thinning at age 22 (251 Mpa and 90 Mpa), then the trend scenario (231 Mpa 87 Mpa) and finally the intensive scenario (216 Mpa 83 Mpa). As expected, more intense and earlier thinnings resulted in lower stress levels. The higher stress in the less intensive scenarios also contributed to higher stress-induced mortality, but it was difficult to dissociate it from the direct effect of the reduction in the number of trees by the interventions.

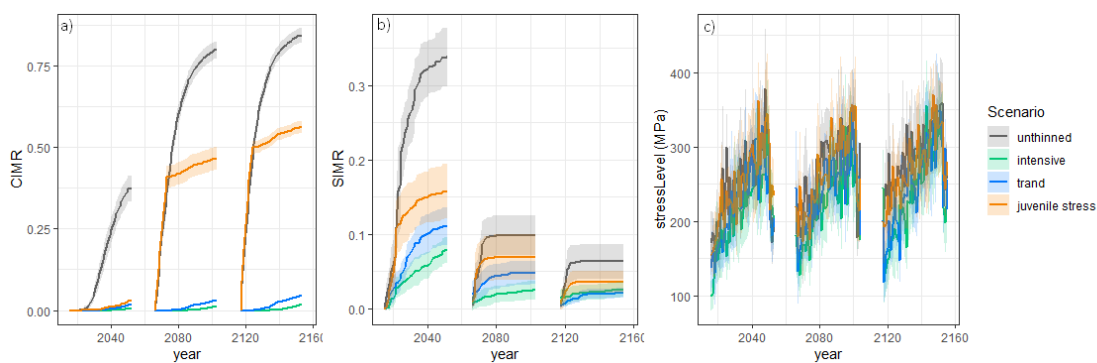


Figure 5. Impact of the silvicultural scenario on the competition-induced mortality rate per silvicultural cycle (a), the stress-induced mortality rate per silvicultural cycle (b), and the stress level during three silvicultural cycles with intense disturbance regime and reference genetic variance (Supp. Figure B1 and B2 for the other stress regimes). The four scenarios are represented by colours, as indicated in the legend. The shaded area represents the 95% confidence interval among the 10 replicates. The pre-recruitment period is deliberately not represented because it constitutes a modelling artefact.

3.3. Overall genetic evolution after three cycles and their consequences on stand performance

Over three silvicultural cycles, the unthinned scenario led to the maximum genetic gain in vigour and lower sensitivity among the four silvicultural scenarios whatever the disturbance regime (Figure 6). The more intensive the silviculture, the higher reduction in evolutionary rate of vigour and sensitivity. The juvenile stress scenario was close to the unthinned scenario with, in comparison, a genetic gain reduced on average by 1% in lower sensitivity (resp. 3% for vigour) over all the disturbance regimes and genetic variances (except zero variance and, for sensitivity, null disturbance regime). Next came the trend scenario with a reduced genetic gain of 17% in lower sensitivity (resp. 33%). Finally came the intensive scenario with a reduced genetic gain in lower sensitivity of 30% (resp. 45%).

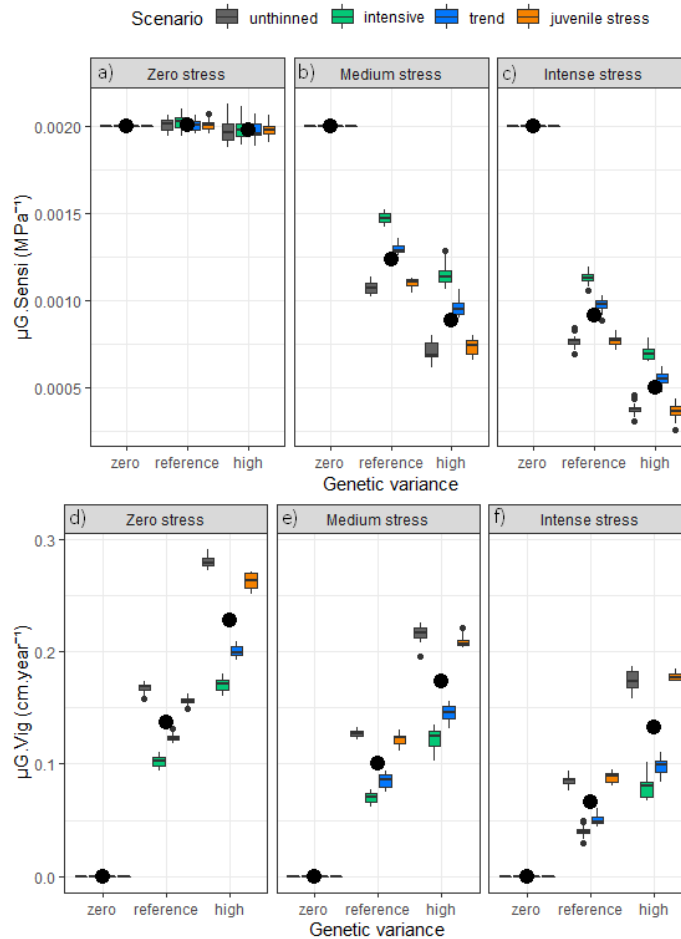


Figure 6. Overall genetic gain in lower sensitivity (a, b, c) and vigour (d, e, f) at the end of the three silvicultural cycles in four silvicultural scenarios, as a function of genetic variance (x-axis) and disturbance regime (panels). The four scenarios are represented by colours, as indicated in the legend.

The dominant diameter predicted by the original growth model without disturbance and without genetic variation in vigour nor sensitivity was little sensitive to the silvicultural scenario, i.e. to the level of stand competition (Figure 7a). With disturbance, and without genetic variation in vigour nor sensitivity, the largest dominant diameter after three silvicultural cycles was observed for the intensive scenario, followed by the trend, then the juvenile stress and finally the unthinned scenario (Figure 7b, c). By contrast, with genetic variation, we found the opposite result whatever the disturbance regime: the largest dominant diameter was obtained with the unthinned scenario, followed closely by the juvenile stress scenario, then the trend scenario and finally the intensive scenario (Figure 7a, b, c). Overall, the initial genetic variance had a greater effect on the dominant diameter than the silvicultural scenario (Figure 7). The basic model (without disturbance and genetic variability) predicts a basal area production strongly affected by the silvicultural scenario, i.e. by stand structure such as the number of trees per hectare (Figure 1; Figure 7d). Whatever the disturbance regimes and initial genetic variances, the largest basal area production is observed for the unthinned scenario, followed by the juvenile stress

scenario, then the trend scenario and finally the intensive scenario (Figure 7d, e, f). Overall, the silvicultural scenario had a greater effect on the basal area production than the initial genetic variance (Figure 7d, e, f).

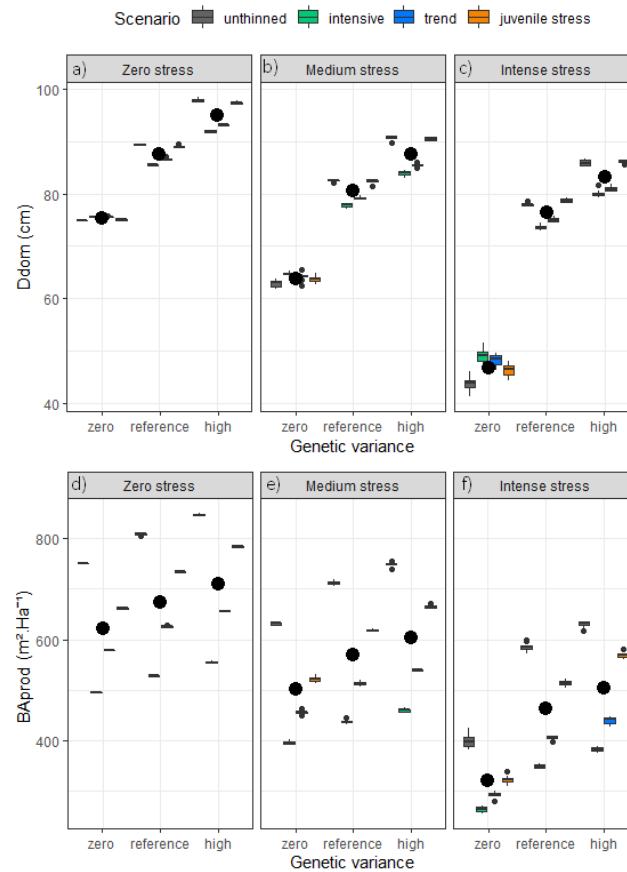


Figure 7. Stand growth performance in terms of dominant diameter (a, b, c) and basal area production (d, e, f) at the end of the three silvicultural cycles in four silvicultural scenarios, as a function of genetic variance (x-axis) and disturbance regime (panels). The four scenarios are represented by colours, as indicated in the legend. The black circles correspond to the mean by initial genetic variance over the silvicultural scenarios.

4. Discussion

4.1. Mechanisms of selection by competition and drought-like disturbances

Using a demo-genetic modelling framework, we quantified the potential response to selection on growth vigour and sensitivity to water stress over three generations in naturally regenerated forest stands subjected to different drought-like disturbance regimes. The process of selection on growth vigour and sensitivity is not prescribed as such in the model but results from the demographic processes,

i.e. self-thinning, stress-induced mortality and differential reproduction. In the unthinned scenario, the only interventions applied, i.e. the seeding cut and the final harvest, are both random cuts that do not impact the genetic values as such and only define the generation time, which evolutionary consequences are outside the focus of this study.

Over three generations, we observed a rapid genetic gain in vigour and, with disturbances, lower sensitivity due to viability selection by competition, viability selection by stress to a lesser extent and, negligibly, fecundity selection. Empirical microevolution studies typically find evolutionary rates (H_0) ranging between 0.1 and 0.3 SD per generation (Hendry et al., 2008; Gingerich 2009). In our simulations, when the considered trait is under selection, we obtained an evolutionary rate varying between 0.181 and 0.416 in absolute value.

Here, we considered two evolvable traits, growth vigour and sensitivity, with multiple selection pressures: competition-induced viability selection, fecundity selection and anthropogenic selection (i.e. selective thinnings) acting on both traits, and stress-induced viability selection on sensitivity only. In this context, eco-evolutionary feedback results from the effect of selection on the correlation between traits and the effect of the correlation on the response to selection. Our simulations were initiated with no initial genetic correlations and no pleiotropy, i.e. the model only accounts for emerging correlations that would dynamically result from the demo-genetic processes. A genetic trade-off at population scale between vigour and sensitivity has often been reported in multisite common garden experiments: provenances that grow best in a favourable site generally grow less than others under stressful conditions (e.g. *Pinus contorta* and *P. sylvestris* in Rehfeldt et al., 2001; 2002). At within-population scale, a phenotypic trade-off between growth vigour and sensitivity was observed in *Abies alba* by Nourtier et al., (2014), in *Cedrus atlantica* by Fallour-Rubio et al., (2009) and in Douglas-fir by Fririon et al., (2023). Other sources of genetic correlations could further restrain the response to selection and contribute to maintaining the variability on both adaptive traits (Pujol et al., 2018).

Adaptive phenotypic plasticity, which could also slow down directional selection against sensitivity by buffering the effects of stress (Paenke et al., 2007; Nicotra et al., 2010; Cailleret et al., 2014), is not explicitly simulated in Luberon2. In addition, the probability of stress-induced mortality is not modulated by the social status of individuals in the model, whereas tall and dominant trees are generally more susceptible to water stress (Bennett et al., 2015), which corresponds to a negative selection on tree size that would reduce selection intensity for vigour and against sensitivity.

We observed a reduced genetic gain on vigour in the presence of disturbances. Thereby, we highlighted a mechanistic trade-off between selection for vigour and against sensitivity resulting from

two processes. First, the relative contribution of vigour to the overall tree growth decreases with increasing stress level and, in addition, selection by stress competes with selection by competition, for a given level of available genetic diversity. In a microheterogeneous environment, this antagonistic selection could lead to linkage disequilibrium and genetic correlations and participate in the phenotypic trade-off between growth vigour and sensitivity observed within stands (e.g. Fririon et al., 2023; Nourtier et al., 2014; Fallour-Rubio et al., 2009), as follows. In microsites with low available water and/or high evapotranspiration, i.e. high LAI, trees may experience higher drought stress than average which may result in stronger selection against sensitivity thus weaker for vigour, and vice-versa in microsites with high available water and/or low LAI (Davi et al., 2008). Moreover, by the same mechanism on a larger scale, this could also participate in generating genetic trade-off as often observed among stand therefore globally in the differentiation of populations in terms of vigour and sensitivity (e.g. Rehfeldt et al., 2001; 2002).

4.2. Considering genetic diversity and evolvability in risk management and productivity

In a recent study, Pretzsch (2021) had quantified the instant benefits of intraspecific genetic diversification in terms of stand growth and stability, analogously to species mixing. In our simulations, we explored the potential benefits of dynamic changes in the genetic composition within- and across generations of trees. In the presence of disturbances, our results show that an adaptive response to selection can occur rapidly and improve stand performances. Evolutionary benefits were visible within the very first silvicultural cycle with a dominant diameter up to 1.61 times greater and a stand biomass production (i.e. basal area production) up to 1.27 times higher with genetic diversity than without. This result highlights that within-stand genetic variability of fitness-related traits is important to consider as the mean value for reducing stand vulnerability. In addition to this short-term reduction of stand vulnerability through genetic sorting within each forest cycle, the realisation of the adaptive potential occurs on the multi-generational scale and our simulations showed a rapid genetic evolution in stand performances over generations. In only three generations, the dominant diameter rose up to two times greater and stand biomass production up to 1.6 times greater with genetic diversity than without, while stress-induced mortality rate decreased from 39% to 8%. These potential benefits both in terms of growth performance and survival to disturbance deserve consideration in management strategies for wood production, carbon storage and other forestry objectives. Thus, our simulations provide a first quantitative assessment of potential genetic gain and trajectory of adaptive genetic diversity in a natural regeneration system, which is adapted and specific to local environmental conditions (especially in the case of strong genotype \times environment interactions).

4.3. Silviculture as an eco-evolutionary lever

Even in a short evolutionary timespan limited to three silvicultural cycles, different silviculture scenarios result in different genetic gains and these differences depend on the disturbance regime. Silviculture has a double role in evolution: it is a regulator of natural evolutionary processes (Godineau, Fririon et al., submitted) and it can also be a direct driver of anthropogenic selection as shown in our simulations. Here, thinning was systematically done from below, and therefore directional selection on tree size by silviculture was strictly aligned with viability selection by self-thinning and fecundity selection. In reality, foresters may use multiple criteria to choose the trees to harvest or to leave, resulting, regarding tree size, in thinning from below, from above or randomly, depending on forestry objective, stand stage and personal forester's judgement. Thus, our simulations shed new light on the global trends and mechanisms of genetic impact of selection by silviculture, even though the evolutionary rates simulated here may be slightly overestimated, as previously discussed.

Here, the unthinned scenario represented the maximum genetic gains and silvicultural interventions reduced them: the more intensive the silviculture, i.e. the more intense and earlier thinnings, the higher reduction in evolutionary rates. This result can be explained by two mechanisms. First, by reducing the LAI, silvicultural interventions reduced both competition intensity, a joint selection pressure on vigour and sensitivity, and stress levels, a selection pressure specifically against sensitivity under severe drought stress. Therefore, this mechanism should reduce the overall selection pressure more on sensitivity than on vigour, particularly under intense stress regime. We expect to underestimate this reduction of LAI by silviculture in our model because, using an allometric equation to compute individual leaf area from tree diameters, the competition decreases and the remaining trees respond instantly by increasing their leaf area after thinning, whereas in reality several years are necessary to observe this response (Chianucci et al., 2016; Tague et al., 2019). The second mechanism that could explain why intensive silviculture reduced the evolutionary rates is that the first random thinning in the intensive and trend scenarios removed many trees including potentially valuable genotypes, and thus constrained subsequent selection differential. This second mechanism would equally affect the evolutionary rates on vigour and sensitivity. It is difficult to disentangle these two evolution-limiting mechanisms, i.e. limitation by weakened selection pressure vs limitation by random genetic erosion. However, the evolutionary rates of vigour and lower sensitivity were impacted in the same way by the silvicultural scenarios, suggesting that random genetic erosion was the main mechanism of evolutionary limitation by silviculture, while weakening of selection pressure was rather a secondary mechanism.

4.4. Considering eco-evolutionary dynamics in forest management decisions

Our simulations show that silvicultural practices aiming at drought stress through reduction in stand density and LAI (e.g. Sohn et al., 2016; Schmitt et al., 2020; Gavinet et al., 2020; Moreau et al., 2022) should also consider within-stand genetic diversity and evolutionary processes. In the absence of genetic variation, obviously, forest managers cannot rely neither on genetic sorting within a forest cycle nor on genetic evolution across tree generations and the best strategy to promote individual tree growth is to limit the stress level and therefore to move towards a more intensive silviculture. Conversely, when there is within-stand genetic diversity (which is the most common situation except in monoclonal forests), a more intensive silviculture results in a lower dominant diameter from the first silvicultural cycle onwards: strategies that aim to promote spontaneous adaptation have proven to be best in our simulations. Nevertheless, for selection to operate in this way, management must consider and sufficiently preserve genetic diversity. In particular, delaying (or even circumventing) the first silvicultural interventions, like in the juvenile stress scenario, could be an efficient strategy to avoid evolutionary constraints by genetic erosion and to promote genetic adaptation to drought stress since most of the genetic evolution occurs early in the silvicultural cycle. Furthermore, our results show the juvenile stress strategy systematically resulted in higher biomass production, which represents an additional benefit with regard to carbon storage in the ecosystem. In practice, implementing a juvenile stress strategy would generate an over-dense stand at the time of the first effective thinning, requiring particular sequences of interventions starting with more frequent low-intensity thinnings to progressively recover from over-density until trees get bigger and stand structure becomes more robust, when more classical silvicultural sequences can be applied. The juvenile stress strategy was considered here for even-aged forest systems, in a form of temporal balance between natural evolutionary processes and management intensity to reach a compromise between short- and long-term objectives: maintaining stress exposure in the early juvenile stage for long-term adaptation (and acclimation, not considered in our model), while reducing stress exposure later on to limit short-term risk. Similarly, in spatially heterogeneous environments, equivalent approaches aiming to valorize natural selection processes in management would consist in spatially heterogeneous interventions, e.g. allow the most selective areas to contribute to the global evolution of the whole forest (Lefèvre et al., 2014).

The juvenile stress strategy, or its spatial equivalent, can be considered as evolution-oriented forest management strategies (Lefèvre et al, 2014), or more generally an “environmental stewardship” approach (Mathevet et al, 2018), where management considers and drives natural microevolutionary processes. The added benefit of such approaches is constrained by the evolutionary potential of the local genetic resource, but they direct towards adaptation to specific local conditions and thus contribute to adaptive management in the face of the ecological uncertainty (Marmorek et al., 2006; Garmestani & Allen, 2015). However, the juvenile stress strategy may also have negative aspects if some

specific juvenile-mature genetic correlations induce detrimental effects of juvenile selection intensity: such age-age correlations are not considered in the current version of the model. In addition, in practice, management strategies often need to cope with synergies and trade-offs among multiple ecosystem services and hazards which were not considered here (Jactel et al., 2009; Duncker et al., 2012; Seidl et al., 2017). For example, resistance traits to pest insects can be negatively correlated with growth or wood quality traits (Kleinhentz et al., 1998).

More generally, this study illustrates how the agent-based demo-genetic modelling framework (DG-ABM) can be used to integrate eco-evolutionary considerations into adaptive management decisions. In the forestry case, we used this approach to explore different scenarios of environmental change, genetic diversity and silvicultural interventions, and quantitatively assess the eco-evolutionary consequences of current or innovative management strategies.

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VIII - Discussion générale

La section "Discussion générale" est organisée comme suit. Une première partie vise à résumer les principaux résultats en jugeant de leur cohérence dans le cadre des objectifs initiaux de cette étude. Les résultats sont ensuite confrontés à la littérature scientifique, en particulier à la synthèse bibliographique des interactions entre perturbation, gestion et diversité génétique. Mon étude est ensuite analysée de façon critique. Enfin des perspectives pour le modèle Luberon2 et pour des travaux de recherche futurs sont énoncés.

1. Synthèse des principaux résultats scientifiques

1.1. Résumé des travaux réalisés

Une approche originale par modélisation a été développée pour répondre aux objectifs de l'étude à savoir : [1] identifier les processus éco-évolutifs qui façonnent la dynamique forestière et quantifier le potentiel de la diversité génétique et de la microévolution pour atténuer la vulnérabilité d'une population d'arbres aux changements de régimes de perturbations et éventuellement la sauver de l'extinction ; [2] Identifier comment des stratégies de sylviculture adaptative peuvent atténuer la vulnérabilité des forêts au changement climatique sur une échelle de temps écologique comparativement à des recommandations plus classiques et identifier les risques, les coûts et les avantages de ces stratégies pour raisonner d'éventuels compromis.

J'ai formalisé le concept de régime d'impact sécheresse via l'analyse des données de cernes de croissance individuelles de cinq espèces forestières du réseau RENECOFOR. L'intensité du stress est mesurée par le déficit hydrique annuel du sol qui intègre l'aléa climatique (déficit de précipitations) et les facteurs de sensibilité à l'échelle du peuplement que sont la surface foliaire, dynamique, et la réserve utile en eau du sol, fixe. A l'échelle de l'individu, la vigueur définit le potentiel de croissance dans une année sans stress et la sensibilité correspond à la perte de croissance relative par unité de stress. J'ai introduit ce formalisme dans Luberon2, un DG-ABM préexistant initialement calibré pour le cèdre, que j'ai étendu au sapin Douglas.

En parallèle, cette étape de conceptualisation m'a permis d'estimer des variances phénotypiques intra-population de vigueur et de sensibilité au stress hydrique ; estimations utilisées pour déduire les variances génétiques introduites dans les simulations avec l'hypothèse d'une héritabilité de 0,3. Les résultats mettent en évidence une large variation phénotypique en termes de sensibilité et de vigueur et un compromis entre les deux traits de croissance. Si une variation phénotypique élevée au sein des peuplements devrait contribuer à la résilience et à la capacité d'adaptation des forêts au changement climatique, un compromis entre vigueur et moindre sensibilité pourrait, au contraire, représenter une contrainte pour la sélection. Considérer ce compromis dans les décisions de gestion est capital. En particulier là où le stress hydrique n'est pas encore fréquent, il existe un risque de sélectionner excessivement les individus vigoureux mais potentiellement sensibles et ainsi augmenter la vulnérabilité des peuplements au changement climatique. Dans ce cas, des pratiques de gestion soutenant la conservation de la diversité d'arbres à croissance lente et à croissance rapide au sein des populations pourraient être une stratégie pour atténuer les impacts futurs des sécheresses, accroître la résilience et favoriser le potentiel adaptatif.

À partir du modèle Luberon2, j'ai conçu et analysé deux plans de simulation complémentaires répondant chacun à une problématique distincte. Le premier, sans stress hydrique et appliqué au cèdre, illustre que la sélection naturelle dépend étroitement de la compétition densité-dépendante en forêt. En effet, les résultats montrent une augmentation rapide de la vigueur et des performances de croissance des peuplements en réponse à un environnement social compétitif sélectif : les individus moins vigoureux grandissent moins vite, donc se reproduisent moins et ont une chance accrue d'être éliminés par compétition. Une mortalité par perturbations naturelles et/ou anthropiques (éclaircies systématiques) induit une réduction de la compétition. Ainsi, une gestion plus intensive (éclaircies plus nombreuses, plus précoces précoces et systématiques) réduit la sélection naturelle au sein des populations d'arbres, fait aggravé en présence de perturbations naturelles non sélectives. On attend des résultats similaires pour des perturbations non létales réduisant la croissance : une réduction de la croissance devrait réduire la compétition, donc la mortalité par compétition et la sélection associée. Des perturbations affectant seulement la reproduction n'impacteraient pas la sélection par compétition. En outre, les résultats montrent que raccourcir le cycle sylvicole augmente la fréquence de reproduction et donc les opportunités de sélection par la fécondité

(avec des conséquences évolutives qui dépendent de la corrélation entre la vigueur et la fertilité à un stade plus précoce) et concentre la période d'exposition à la compétition à un stade plus précoce où elle est susceptible d'être plus intense (avec des conséquences évolutives qui dépendent de la corrélation entre la vigueur et la croissance juvénile).

Le deuxième plan de simulation, avec stress hydrique et appliqué au sapin Douglas, montre également une réponse rapide à la sélection naturelle en termes de vigueur, et aussi en termes de moindre sensibilité. En effet, en fonction du régime de perturbation, les individus peu vigoureux et/ou sensibles grandissent moins efficacement, donc se reproduisent moins et ont ensuite plus de chance d'être éliminés par la compétition. De plus, lorsque leur croissance annuelle est fortement impactée, les arbres sensibles ont une probabilité accrue d'être éliminés. Les résultats mettent en évidence des mécanismes de sélection antagoniste susceptibles de participer à la mise en place de la corrélation génétique souvent observée entre vigueur et sensibilité : le stress contre-sélectionne les arbres sensibles tout en réduisant les opportunités de sélection par la compétition. La sélection pour une moindre sensibilité induit une augmentation des performances du peuplement en termes de croissance et de survie face au stress appréciable dès la première génération. Ses performances augmentent à chaque génération. Les résultats montrent qu'en l'absence de variation génétique, la meilleure stratégie pour favoriser la croissance est de s'orienter vers une sylviculture plus intensive qui limite le niveau de stress en maintenant un LAI faible. A l'inverse, dès lors qu'il y a de la diversité génétique, c'est-à-dire le cas réaliste sauf plantations monoclonales, une sylviculture moins intensive, visant à favoriser l'adaptation spontanée, représente la meilleure stratégie à court terme (le cycle sylvicole en cours) comme à moyen terme (au delà du cycle en cours). En particulier, le maintien d'un niveau élevé de stress à un stade de peuplement juvénile, en retardant les premières éclaircies, semble être une stratégie prometteuse pour favoriser une acclimatation et une adaptation précoce au stress hydrique tout en maintenant globalement un potentiel évolutif élevé. Néanmoins, la mise en place d'une telle stratégie risque de mener le peuplement à une surdensifié nécessitant une gestion de rattrapage particulière. De plus, son application semble restreinte aux forêts équiennes, c'est-à-dire en peuplement composé d'arbres ayant tous le même âge.

Les résultats majeurs de l'étude synthétisés ici apportent des réponses constructives aux questions posées. Premièrement, sous condition des hypothèses génétiques employées,

les résultats soutiennent qu'une adaptation rapide des forêts est envisageable, en particulier pour réduire la vulnérabilité des populations à un régime de perturbation non catastrophique, avec des effets appréciables sur une échelle de temps écologique. De plus, ils apportent des éléments de compréhension sur la mise en place de la sélection et sur les rétroactions éco-évolutives en forêt. Les modalités du plan de simulation avec stress hydrique n'ont pas provoqué d'effondrement démo-génétique. Aussi, il n'a pas été possible de tester le potentiel de la diversité génétique et de la microévolution pour amorcer un sauvetage évolutif. Deuxièmement, les résultats montrent qu'une sylviculture intensive réduit systématiquement le potentiel évolutif des populations. Mes travaux ont permis de concevoir et de tester une stratégie de gestion originale visant à retarder les premières éclaircies pour favoriser les processus adaptatifs naturels sans perdre sur les performances dendrométriques. Cette stratégie dite de stress juvénile s'est montrée particulièrement efficace pour réduire la vulnérabilité de peuplements de sapin Douglas soumis au stress hydrique. Les risques, les coûts et les bénéfices de son application ont été discutés et devraient, à terme, servir de base pour raisonner de potentiels compromis dans le cadre d'une gestion multi-risque et multi-critère. Globalement, la démarche par modélisation démo-génétique individu-centrée proposée a permis de mieux comprendre les rétroactions éco-évolutives en forêt et de présenter le potentiel adaptatif comme une caractéristique dynamique et évolutive de la population.

1.2. Confrontation de l'étude avec la littérature scientifique

1.2.1. Sur les capacités de microévolution des peuplements forestiers

Cette étude apporte une quantification de la variation interindividuelle au sein des populations d'arbres forestiers et de son rôle dans l'adaptation au changement climatique. Mes travaux s'inscrivent dans une littérature grandissante qui montre que des réponses démographiques, écologiques et évolutives peuvent toutes se produire et interagir sur une échelle de temps écologique, sur quelques générations seulement, lorsque la sélection est forte (Pelletier et al. 2009 ; Hendry 2017 ; Govaert et al. 2019). Les taux d'évolution produits par le modèle se trouvent dans la gamme des études empiriques de microévolution (Hendry et al., 2008 ; Gingerich 2009 ; Gorné & Diaz, 2017, 2019), argument fort pour la validation du modèle et pour la pertinence des résultats. Néanmoins, il existe très peu d'études prédictives sur les capacités d'évolutions des peuplements forestiers auxquels confronter mes travaux. En outre,

les traits considérés (vigueur et sensibilité) sont peu étudiés par les écologues évolutifs. Notamment, la vigueur est souvent considérée comme un trait de forestier productiviste alors même que son lien avec la survie est bien illustré par la littérature récente de dendrochronologie.

1.2.2. Sur les conséquences démo-génétiques de la gestion des peuplements

Dans les populations exploitées, les individus prélevés, par exemple par la chasse ou la pêche, sont généralement ceux à haute valeur sélective du point de vue de l'exploitation : les plus beaux et/ou les plus grands (Coltman, 2003 ; Chiyo et al., 2015 ; Bouffet-Halle et al., 2021). Ainsi, il y a un risque de contre sélectionner les meilleurs génotypes avec des conséquences néfastes rapides sur les performances de la population. La gestion forestière, quant à elle, consiste en la conduite du peuplement à chaque étape de son développement, avec l'avantage de pouvoir favoriser très tôt les phénotypes les plus performants en éliminant les moins bons dans un objectif de production et/ou d'adaptation. Dans ce cas, la gestion n'est pas réduite à une exploitation sélective, les forestiers parlent même d'interventions d'amélioration du peuplement. Ces interventions jouent aussi sur le plan génétique. Néanmoins, les interventions non sélectives restent courantes et ont pour conséquence de réduire l'intensité des sélections portant sur des traits corrélés à la dimension des arbres. Les impacts du prélèvement d'individus sur la sélection densité-dépendante avait déjà été décrite chez d'autres organismes avec des résultats semblables, par exemple chez des poissons (Bouffet-Halle et al., 2021). A ma connaissance, les travaux réalisés dans le cadre de ma thèse sont les premiers à traiter de cette problématique chez des arbres forestiers. Mes résultats ne se cantonnent pas au cèdre et au sapin Douglas. En effet, la dynamique des peuplements forestiers tend de façon générale à abaisser progressivement le rang social des arbres à faible croissance puis, en particulier pour les espèces intolérantes à l'ombre, à les éliminer par compétition (Hülsmann et al., 2018).

Faces aux sécheresses, la littérature existante incite généralement à l'intensification de la sylviculture pour réduire le stress hydrique et ses conséquences à court terme sur la croissance et la survie des arbres (Sohn et al., 2016 ; Schmitt et al., 2020, Gavinet et al., 2020 ; Moreau et al., 2022). Luberon2 a montré une bonne aptitude à reproduire ces mécanismes. Néanmoins, les antagonismes entre les effets de la gestion à court terme (réduction de l'exposition au stress) et à long terme (limitation de l'acclimatation et l'adaptation) identifiés

dans cette étude invitent nécessairement à repenser ces pratiques. En particulier, pour des forêts en régénération naturelle, mes travaux sont en désaccord avec des stratégies d'éclaircies juvéniles visant à atténuer l'effet à court terme des sécheresses dans les jeunes forêts, comme proposé par Wang et al. (2019), qui ne tiennent pas compte des aspects évolutifs à plus long terme. En effet, conformément aux attentes théoriques, mes résultats suggèrent que plus les éclaircies seront appliquées précocement, plus elles auront un impact important sur la qualité génétique du peuplement puisqu'elles empêchent une grande partie de la sélection naturelle de se produire (Lefèvre et al., 2014). Ce résultat, obtenu en considérant un stress à effet quantitatif généralement non léthal, permet d'étendre les conclusions de Kuparinen et al. (2010) qui avaient montré par simulation théorique que la réduction systématique du taux de mortalité est un frein évolutif majeur. Aussi, maintenir dans un premier temps une période de forte sélection naturelle (sur la croissance et la survie) et réduire ensuite le stress par des éclaircies est une stratégie prometteuse et applicable à une multitude de facteurs de stress dès lors qu'une réponse adaptative rapide est possible (Jactel et al., 2009 ; Moreau et al., 2022). Outre la différenciation temporelle entre maintenir et réduire le stress au sein d'un même peuplement, on peut envisager une différenciation dans l'espace à l'échelle du massif forestier : des parcelles à faible densité pour produire sans risque immédiat, et des parcelles à forte densité pour sélectionner sur le long terme.

Une autre stratégie d'adaptation au changement climatique consiste à avancer la première éclaircie pour réduire la durée du cycle de production, et donc diminuer la période d'exposition du peuplement aux stress (Legay et al., 2015). Mes travaux mettent en avant le potentiel d'un raccourcissement du cycle sylvicole pour favoriser l'adaptation. Néanmoins, ici l'objectif de production contraint à accompagner le raccourcissement du cycle sylvicole d'une intensification de la gestion. Il convient de mettre en garde quant aux impacts négatifs attendus de cette intensification sur les processus évolutifs, sur la qualité génétique et sur les performances des peuplements. Des compromis entre objectif de production et objectif de réduction des risques doivent être trouvés. Lorsque c'est envisageable, je préconise de raccourcir le cycle sans intensifier la sylviculture. Néanmoins, et pour rester pertinentes, ces recommandations doivent être considérées dans un cadre multi-critère par le gestionnaire (considérer l'impact sur les sols, par exemple).

2. Analyse critique de l'étude

2.1. Pertinence des sorties du modèle Luberon2

Luberon2 génère des corrélations génétiques positives émergentes entre vigueur et sensibilité (voir également Copie, 2022), qui correspondent à ce qu'on observe *in situ*. Ce résultat est intéressant car il montre que ces corrélations peuvent émerger des rétroactions éco-évolutives liées à la dynamique démo-génétique des peuplements et que le modèle permet de rendre compte de tels mécanismes.

Dans les simulations, la sélection naturelle s'appuie sur des corrélations positives des performances génétiques individuelles (vigueur et sensibilité) avec à la fois la capacité de compétition et la fertilité. En réalité, d'autres processus non inclus dans le modèle pourraient réduire ces corrélations, par exemple, des compromis d'allocation des ressources entre les fonctions de croissance et de reproduction (Wardlaw, 1990), des compromis phénotypiques entre la vigueur et la sensibilité au stress (Fririon et al., 2023) ou des compromis du cycle biologique entre la croissance et la longévité (Roskilly et al., 2019). La plasticité phénotypique adaptative pourrait également impacter la sélection directionnelle contre la sensibilité en atténuant les effets du stress et en modifiant la relation entre génotype et phénotype (Paenke et al., 2007 ; Nicotra et al., 2010 ; Cailleret et al., 2014). Pour finir, les arbres dominants sont généralement plus sensibles au stress hydrique (Bennett et al., 2015), ce qui pourrait être un frein à la sélection sur les performances de croissance. Les conséquences ultimes de ces processus sur la corrélation entre la vigueur et la valeur sélective, c'est-à-dire le gradient de sélection, sont difficilement prévisibles car ce gradient de sélection résulte dynamiquement d'interactions complexes entre plusieurs processus. Par conséquent, les taux d'évolution obtenus dans cette étude correspondent à un niveau de sélection limite supérieur, mais toujours plausible.

Le développement d'un modèle démo-génétique requiert des données sur de nombreux processus. La calibration de ce type de modèles est complexe en raison du manque de données expérimentales. Par conséquent, un certain nombre de mécanismes relatifs à la reproduction et ayant un impact reconnu sur les processus évolutifs ne sont pas pris en compte. Il s'agit notamment de l'intensité du masting, la phénologie de reproduction qui module la

panmixie et l'apparemment, les différences individuelles de floraison entre cônes mâles et femelles, l'impact de la consanguinité sur les performances individuelles, d'autres, influencés par les choix de gestion, sont énoncés par Lefèvre et al. (2014). Aussi, les fonctions de fécondité mâle et femelle ainsi que les fonctions de dispersion du pollen et des graines du cèdre sont utilisées pour le sapin Douglas.

2.2. Considérations dans le cadre de l'approche multirisques

Dans le cadre de mes travaux, j'ai formalisé la notion de régime d'impact sécheresse et l'ai implémenté dans Luberon2 pour étudier ses conséquences sur la dynamique démographique des peuplements forestiers. En réalité, un peuplement forestier est soumis à de multiples régimes de stress biotiques et abiotiques (gelés tardives, canicules, rougissement physiologique, incendies, tempêtes, chablis, épidémies, multiples ravageurs etc.). L'évaluation globale du risque nécessite donc la mise en place d'une approche multidisciplinaire et multirisque pour tenir compte des multiples effets d'interaction entre perturbations, notamment au travers de la gestion (par ex. des effets antagonistes sur différents aléas) et du paysage génétique (par ex. des compromis de résistance à différents stress). Luberon2 permet d'intégrer différents types d'impacts de perturbations sur la croissance (et ses conséquences sur la survie et la reproduction), sur la mortalité indépendamment de la croissance ou sur la reproduction indépendamment de la croissance. Pour chacun de ces impacts, le modèle permet d'intégrer ou non une variabilité génétique de la sensibilité. Des corrélations mécaniques entre les processus démographiques liés à différents impacts peuvent induire des relations de pléiotropie médiées entre les gènes contrôlant différentes sensibilités, tandis que la dynamique évolutive peut faire émerger des corrélations "dynamiques" par déséquilibre de liaison entre ces mêmes gènes.

Lorsque les perturbations sont multiples mais considérées comme indépendantes, l'évaluation du risque global s'effectue en établissant la liste des perturbations qui pourraient affecter le système considéré, puis en cumulant les dommages prédits en ignorant les potentiels effets de synergie et cascades de risque. Dans ce cadre purement additif, le formalisme de régime d'impact sécheresse proposé dans le cadre de mes travaux a été pensé pour être facilement transposable à tout autres aléas abiotiques et biotiques. Dans le temps imparti pour réaliser ma thèse, il n'a malheureusement pas été possible de calibrer de régime

d'impact supplémentaire pour tester les effets, potentiellement antagonistes, de la gestion et de la sélection sur des facteurs de perturbation multiples.

Les interactions entre différents types de perturbations sont rarement, sinon jamais, nulles (Seidl et al., 2017). Le cadre de l'approche multirisques prend en compte ces interactions et les effets de cascade qui amènent souvent à des dommages exacerbés. Par exemple, à la suite d'une sécheresse ou de sécheresses répétées, les scolytes peuvent se reproduire massivement sur les arbres affaiblis, conduisant à une explosion de leur population et à des dépérissements. Les galeries de scolytes sont alors autant de portes d'entrée pour d'autres organismes saproxyliques ou des pathogènes. Conséquence globale, des événements de mortalité peuvent se produire et générer du combustible qui alimente le risque incendie. L'aléa sécheresse a donc une position plutôt en amont dans les cascades de risques (Seidl et al., 2017). Ainsi, agir sur la vulnérabilité aux sécheresses permet *a priori* de réduire l'impact de toutes les perturbations plus en aval de la cascade de risque, et d'appréhender la gestion du risque en forêt de façon plus globale.

3. Perspectives

3.1. *Luberon2, un outil pour les gestionnaires*

Pour les gestionnaires, Luberon2 développe un cadre formel d'intégration des connaissances sur (i) la croissance et la dynamique des peuplements forestiers, (ii) les régimes d'impacts de différents aléas, (iii) les déterminants génétiques et la diversité interindividuelle de sensibilité à ces aléas chez les essences implémentées (le cèdre et le sapin Douglas). D'autres essences, notamment de chêne et de sapin, seront implémentées. Cet outil permet d'évaluer différentes options de gestion du point de vue de leurs impacts sur la croissance, la dynamique démographique et la diversité génétique, sous différents scénarios de régimes de perturbations. Cet outil est principalement dédié aux services R&D des entreprises forestières publiques et privées familiarisées avec la plateforme de modélisation Capsis. Ces utilisateurs ont la possibilité d'utiliser tous les outils de simulation d'intervention proposés par la plateforme et de créer de nouveaux fichiers d'inventaire initial pour concevoir leurs propres études. Luberon2 vise ainsi à apporter une aide aux gestionnaires forestiers pour répondre à des objectifs d'adaptation et de conservation génétique lors des interventions et traitements

sylvicoles. En plus de l'utilisation directe du modèle, toute la communauté Capsis peut librement réutiliser le code source, dans le respect de la charte Capsis. L'environnement graphique interactif est intuitif et permet une utilisation simple par des personnes non familiarisées avec le logiciel, par exemple pour des formations ou des ateliers pratiques. Le modèle est disponible sur demande.

3.2. Vers des régimes de perturbation non stationnaires

Mes travaux démontrent la grande capacité d'adaptation des populations d'arbres forestiers. Cependant, une question demeure : est-ce que ce sera suffisant pour compenser une altération rapide de régime de perturbation ? En effet, les régimes de perturbation utilisés dans le cadre de mes travaux sont strictement stationnaires. La version actuelle du module d'impact de Luberon2 ne permet pas de reproduire une dérive climatique, et, pour répondre à cette question, une nouvelle phase de développement sera nécessaire. Le stress est actuellement tiré dans une distribution de probabilité. Techniquement, il s'agira de faire dériver les paramètres de cette distribution dans le temps afin d'augmenter progressivement la probabilité de tirer des valeurs de stress élevées. La vitesse de la dérive sera à déterminer sur la base de données climatiques passées, contemporaines et futures. En outre, les processus menant à l'effondrement démographique des populations ne sont pas correctement représentés dans la version actuelle, car le nombre de graines produites à la régénération est arbitraire et maintient artificiellement en place la population à chaque génération. C'est un point qu'il faudra résoudre pour traiter des questions d'effondrement. De plus, des impacts directs de la sécheresse sur la survie et sur la fertilité mâle ou femelle non liés à la réduction de croissance ne sont pas pris en compte mais participent au risque d'effondrement.

3.3. Stratégie d'enrichissement génétique et mélange de populations

Une stratégie supplémentaire possible pour l'adaptation au changement climatique consisterait à associer une gestion qui favorise l'adaptation à un enrichissement de la diversité locale à partir d'une certaine quantité (à déterminer) de matériel génétique allochtone d'une origine présumée pré-adaptée, par l'introduction d'arbres, de graines ou de pollen. Luberon2 permet de simuler des mélanges de populations différenciées génétiquement, et des travaux

ont débuté quant à l'étude des mécanismes évolutifs post-mélange de populations de cèdres dans le cadre d'un stage de fin d'étude que j'ai co-encadré (Copie, 2022).

Conclusion générale

Les connaissances sur le rôle de la diversité génétique et de la micro-évolution dans la réduction de la vulnérabilité des écosystèmes forestiers à l'altération des régimes de perturbation est un enjeu majeur dans le contexte de changement climatique. En outre, les impacts des pratiques de gestion méritent d'être intégrés dans cette réflexion, car les interventions humaines modifient la pression de sélection environnementale, la capacité d'adaptation, et globalement l'ensemble des facteurs de vulnérabilité des populations. Les progrès dans ces domaines doivent permettre d'améliorer les connaissances théoriques sur la mise en place de la sélection naturelle et des rétroactions éco-évolutives et d'élaborer des stratégies de gestion pérennes qui favorisent ces processus.

Les traits de vigueur et de sensibilité au stress en termes de croissance ont été formalisés, et leur variation intra-population a été analysée dans des peuplements du réseau RENECOFOR. Nous émettons l'hypothèse que la large diversité inter-individuelle observée pour ces deux traits contribue à la résilience et à la capacité d'adaptation des forêts. Néanmoins, le compromis observé entre vigueur et moindre sensibilité pourrait représenter une contrainte sélective. Nous estimons important de considérer ce compromis dans les décisions de gestion, en particulier pour éviter de sélectionner excessivement des individus vigoureux mais sensibles et ainsi augmenter la vulnérabilité des peuplements au changement climatique.

Le rôle de la micro-évolution pour réduire la vulnérabilité des populations d'arbres forestiers et l'impact de la gestion sylvicole ont été quantifiés à l'aide du modèle Luberon2, calibré pour le cèdre et le sapin Douglas, qui simule conjointement l'effet de régimes de perturbations et d'interventions sylvicoles sur la dynamique démo-génétique de peuplements monospécifiques. En outre, ce modèle offre un outil d'aide à la décision pour les gestionnaires qui souhaitent intégrer les processus évolutifs dans leurs réflexions.

L'examen approfondi de la dynamique démo-génétique des peuplements révèle que la compétition densité-dépendante est le moteur principal de la sélection des traits relatifs à la croissance des arbres (vigueur, sensibilité et traits corrélés). Nous montrons qu'une réponse sélective rapide, associée à une augmentation des performances de croissance et de survie face au stress, est possible sur une échelle de temps écologique lorsque la sélection est forte. Nous

soutenons qu'il est capital de maintenir, voire même faciliter, ces processus de sélection naturelle pour réduire la vulnérabilité des forêts aux changements environnementaux.

L'impact de différents itinéraires sylvicoles classiques et originaux sur la dynamique démo-génétique a été simulé. Nous montrons que, l'intensification de la gestion (des éclaircies plus nombreuses, plus précoces et plus intenses) limite systématiquement les processus de sélection naturelle. Lorsque les choix de gestion consistent à intensifier la sylviculture pour réduire l'intensité du stress lors de perturbations, notamment de sécheresses, il convient donc de mettre en garde quant aux impacts négatifs à court et moyen terme sur la valeur génétique et sur les performances des peuplements, notamment la sensibilité aux aléas. Nous montrons qu'il est possible de réduire efficacement ces impacts par ajustement des itinéraires sylvicoles classiques. En particulier, nous recommandons de retarder les premières éclaircies pour instaurer une période de non-intervention qui maintient un niveau de stress élevé, favorisant ainsi les processus naturels d'acclimatation et de sélection.

La poursuite du développement de Luberon2 devrait permettre d'étudier la réponse évolutive aux régimes de perturbation non stationnaires reproduisant la dérive climatique actuelle. Par ailleurs, il nous semble nécessaire de considérer et de tester d'autres stratégies prometteuses basées sur les processus évolutifs tels que l'enrichissement de la ressource génétique locale par l'introduction de matériel génétique allochtone présumé pré-adapté.

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<https://doi.org/10.1126/science.1192666>
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Annexe 1 : annexes des articles

Article 1. Figures et Tableaux supplémentaires (S1 à S3)

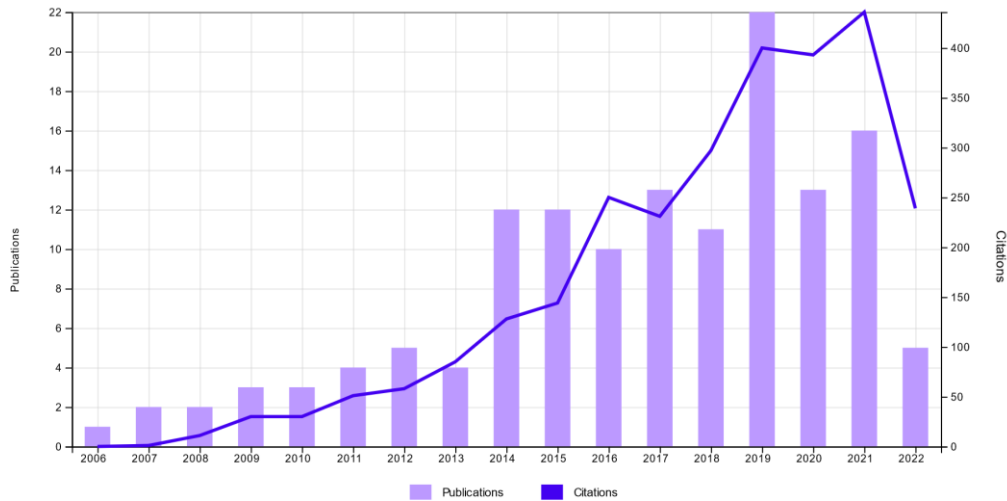


Figure S1a. Distribution over time of the 138 selected publications associated to “IBM” and “eco-evolution” keywords. Keywords: (Individual-based model* OR IBM)* AND (eco-evol* OR demo-genet* OR demogenet* OR ecogenet* OR eco-genet*). WOS 1955/01/01-2022/07/01.

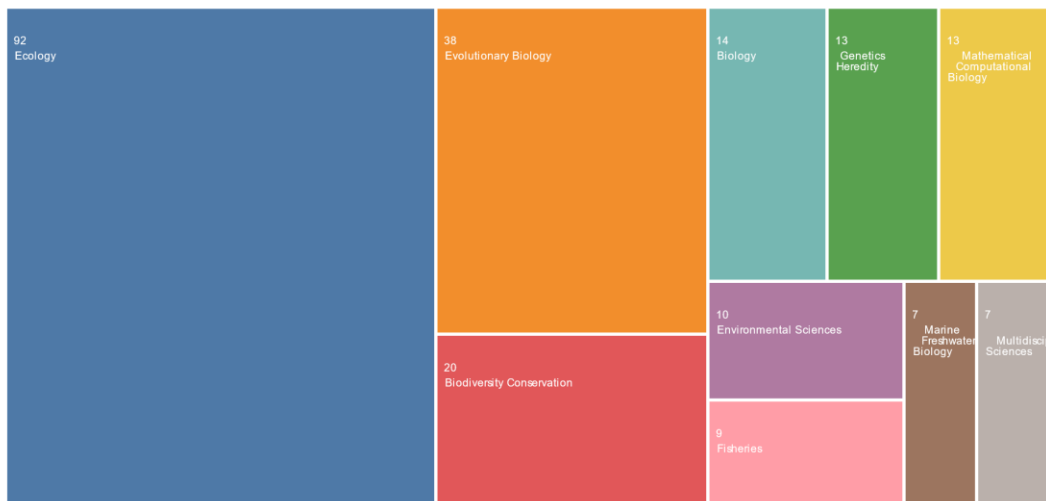


Figure S1b. WOS categories of the 138 selected publications associated to “IBM” and “eco-evolution” keywords. Keywords: (Individual based model* OR IBM)* AND (eco evol * OR demo genet* OR demogenet * OR ecogenet * OR eco genet*). WOS 1955/01/01-2022/07/01.

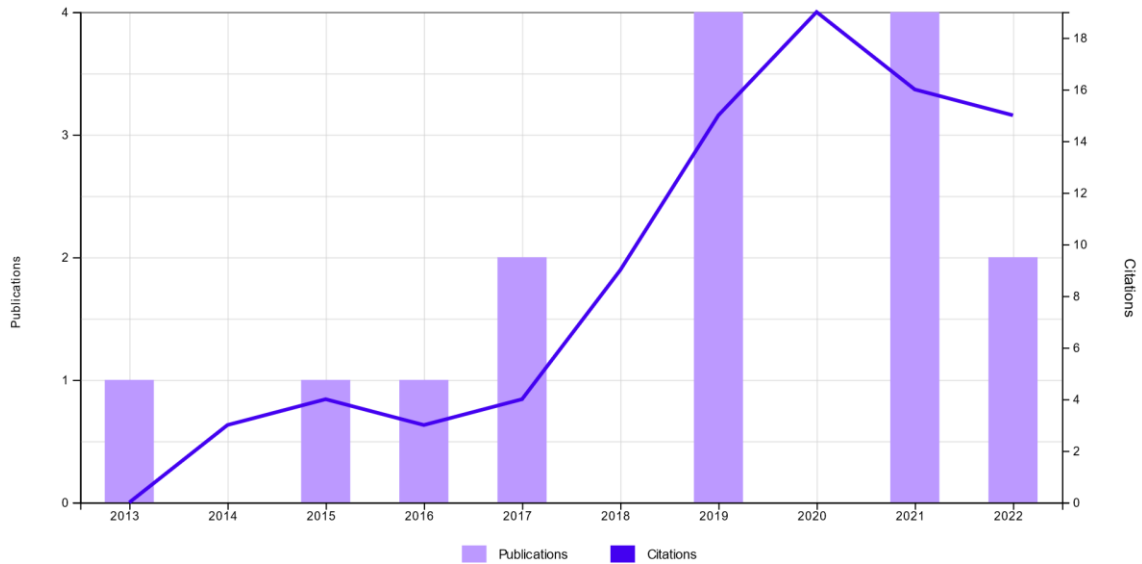


Figure S1c. Distribution over time of the 15 selected publications associated to “ABM” and “ecoevolution” keywords. Keywords: (Agent based model* OR ABM)* AND (eco evol * OR demo genet* OR demogenet * OR ecogenet * OR eco genet*). WOS 1955/01/01 2022/07/01.



Figure S1d. WOS categories of the 15 selected publications associated to “ABM” and “ecoevolution” keywords. Keywords: (Agentbased model* OR ABM)* AND (eco evol * OR demo genet* OR demogenet * OR ecogenet * OR eco genet*). WOS 1955/01/01 2022/07/01.

Table S2. Publications excluded during the literature review.

This table focuses on original publications of models that were not retained. The sub-categories a) to d) correspond to other models than IBMs. The sub-category e) corresponds to models applied on a time scale of maximum 1 generation, i.e., without evolution. The sub-category f) corresponds to models which do not represent neither explicit nor implicit interactions between conspecific individuals. Finally, the sub-category g) corresponds to models including interindividual interactions, but either without individual variation in the interaction-related trait(s), or with purely plastic variation in these traits.

The category “Not appropriate” gathers: 15 reviews, seven technical publications (introducing a new software without specific investigation of an eco-evolutionary issue), five publications related to cell biology model (without any link to ecology), three book chapters, one conference proceeding, one preprint and one duplicated study.

Category	Sub-Category	Number of publications
Original publication of a new model but...	a) Concept paper	1
	b) Niche model	1
	c) Differential equation model	1
	d) Integral projection model (IPM)	2
	e) ABM without evolution	7
	f) DG-ABM without interactions	16
	g) DG-ABM with interactions but without eco-evolutionary feedback	18
DG-ABM with interindividual interactions affecting fitness		74
Not appropriate (review, software, proceeding publication)		33
Total		153

Data Availability Statement:

Table S1 compiling the 153 publications from the WOS search and Table S3 containing the database of 88 publications will be made available upon publication acceptance at INRAE dataverse (<https://entrepot.recherche.data.gouv.fr/dataverse/>).

Article 2. Échelles spatiales et temporelles dans Luberon2 (1),
Conséquences du choix de la taille des pixels (2), Fonctions de
croissance et de fécondité de Luberon2 (3) et Figures
supplémentaires (4)

Appendix 1 - Spatial and temporal scales in Luberon2

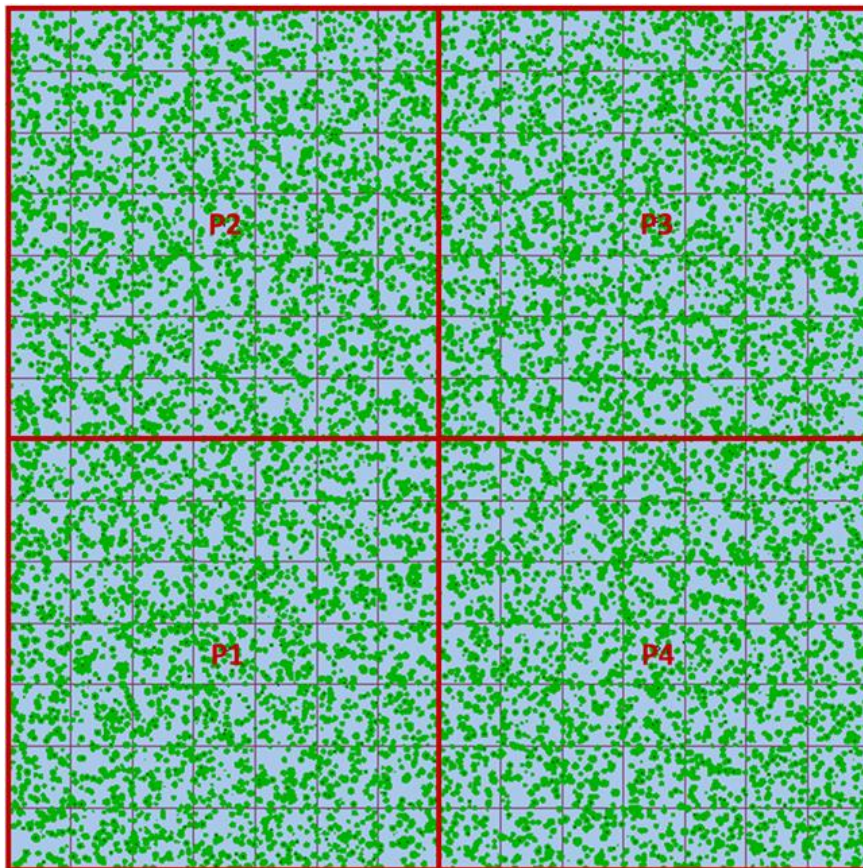


Figure 1: Illustration the simulated *scene* for this study, made of four parcels (P1 to P4, all with the same site index) split in regular *pixels* 15m x 15m (background grid), with 12000 *trees* in the initial stand (green dots with a size proportional to the diameter of each tree).

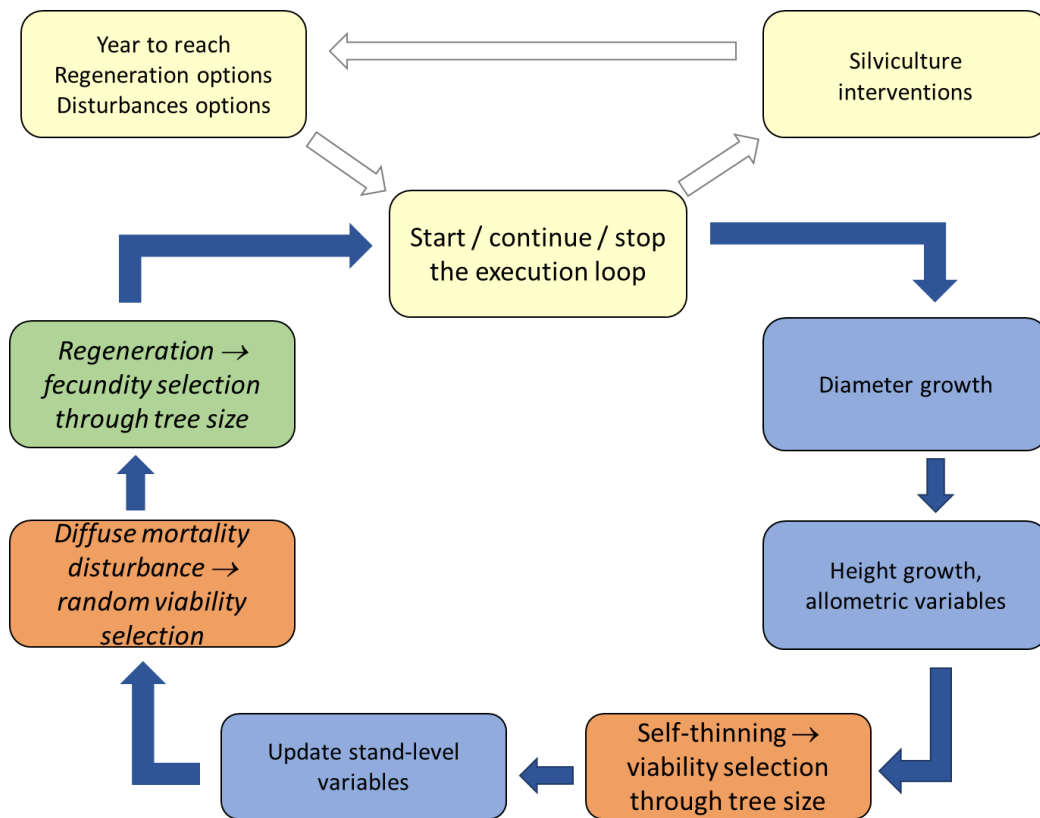


Figure 2: Synthetic view of the execution loop of forest dynamic processes in Luberon2. Yellow boxes represent the user's choices, other colors are for dynamic processes (growth in blue, mortality in orange, and regeneration in green). Regeneration and disturbance (in italics) are optional depending on the user's choices.

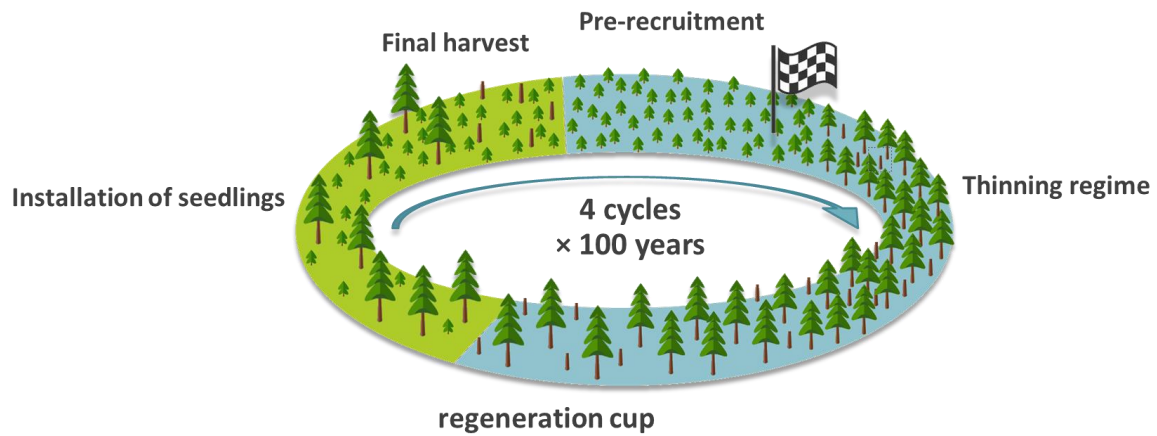


Figure 3. Chronology of a silvicultural cycle: The simulations start with a young 25-year-old stand; the position is indicated by the flag on the diagram. Then the cycle reads clockwise: the population grows ; thinnings are potentially carried out during its development ; when the stand is mature, at 100 years old, a regeneration cut is carried out which will allow the seedlings to settle over a period of three years ; once the seedlings are installed, the final harvesting of the seed trees is done to leave only the seedlings ; the validated range of the growth model begins at 25 years, so, before reaching this age, the seedlings are frozen and no process takes place (this is the so-called pre-recruitment phase by the model). For each simulation, four silvicultural cycle of 100 years follow one another.

Appendix 2 - Consequences of the choice of pixel size

Cette annexe de 22 pages et rédigé par Claire Godineau est disponible en français sur le site de Capsis :

Godineau C., 2017. Choix de la taille idéale des unités de croissance dans Luberon2 et effets de la pixellisation sur l'hétérogénéité spatiale des variables. Internal report.

https://capsis.cirad.fr/capsis/help_en/luberon2

Appendix 3 - Growth and fecundity functions

Individual tree growth

Luberon2 relies on the original growth model calibrated for *Cedrus atlantica* (Courbet, 2002). The basic principle is that current local stand characteristics determine the conditions of individual trees' growth, which in turn determines the future local stand characteristics for the next step. Individual tree growth follows a segmented model where annual increment in basal area is null for trees below a threshold circumference value, and increases linearly with the circumference above this threshold (Figure 1).

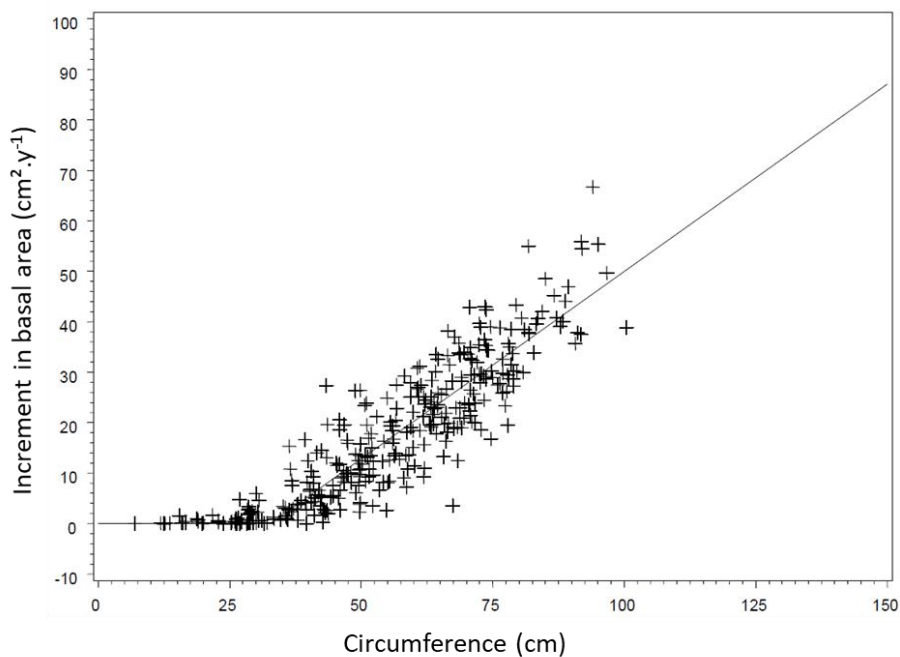


Figure 1. Individual annual increment in basal area as a function of tree circumference in *C. atlantica*: empirical individual data and model prediction (taken from Courbet, 2002).

In Luberon2, this segmented relationship is modeled using the nonlinear function proposed by Perin et al (2017) with three parameters: the threshold value, A , the slope of the relation between annual growth in basal area and circumference, P , and a flexibility parameter smoothing the break around the threshold value, $m (\geq 1)$, resulting in the following equation of growth in basal area (above the threshold):

$$I g_i = 0.5P \left(C_i - mA + \sqrt{(mA + C_i)^2 - 4AC_i} \right)$$

where Ig_i is the increment in basal area of individual i , and C_i the initial circumference. These parameters evolve during stand development, they are dynamically computed for each even-aged growth unit depending on age, stand density and site fertility, as well as species-specific constant values provided as input to the model.

Then, individual phenotypic variation in vigor is added to the diameter growth dD_i as follows:

$$dD_i = \frac{1}{\pi} \left(\sqrt{C_i^2 + 4\pi Ig_i} - C_i \right) + (Mean_vigor + Phenotype_vigor_i)$$

where $Mean_vigor$ is a constant value common to all individuals and $Phenotype_vigor_i$ is the individual phenotypic deviation to this value. Then, knowing the new diameter of each individual tree, allometric relations are used to derive height growth, male and female fecundity variables as well as other values at individual level, such as crown height, or at growth unit level, such as leaf area index.

Female and male fecundity

Trees are considered as fertile from recruitment age and above a threshold DBH value parameterized for each species, i.e. 15cm for cedar and 10cm for Douglas fir. Female fecundity is determined as an ordinal variable related to tree DBH following the model originally calibrated for cedar by Bertrand (2004). Six levels of cone production are defined (in a log-scale) and, each year, the probability to reach each level depends on the DBH, as shown on Figure 2, and crown height. Once the level of cone production is drawn, the actual number of cones produced by this tree in this year is randomly drawn within the range of the fecundity level. Thus, female fecundity has a high inter-annual (for each tree) and inter-individual (among equal-size trees) stochasticity but, currently, there is no synchrony implemented (i.e. masting). The potential number of seedlings generated by each cone produced is set to an estimate of the mean number of viable seeds per cone known for each species.

The probability of a tree i to fall into fecundity level j is given by the following equation:

$$P_i^j = \frac{e^{(m^j - 0.0114DBH_i - 0.3914crown_height_i)}}{1 + e^{(m^j - 0.0114DBH_i - 0.3914crown_height_i)}}$$

where m^j is a constant given for each fecundity level, DBH_i the diameter of the tree in mm and $crown_height_i$ the crown height in m.

Individual “male fecundity” of each fertile tree, which is used to compute the probability of being the father of a recruited seedling (see above), is a relative value simply computed as the square of its DBH (in cm), it is not an absolute value.

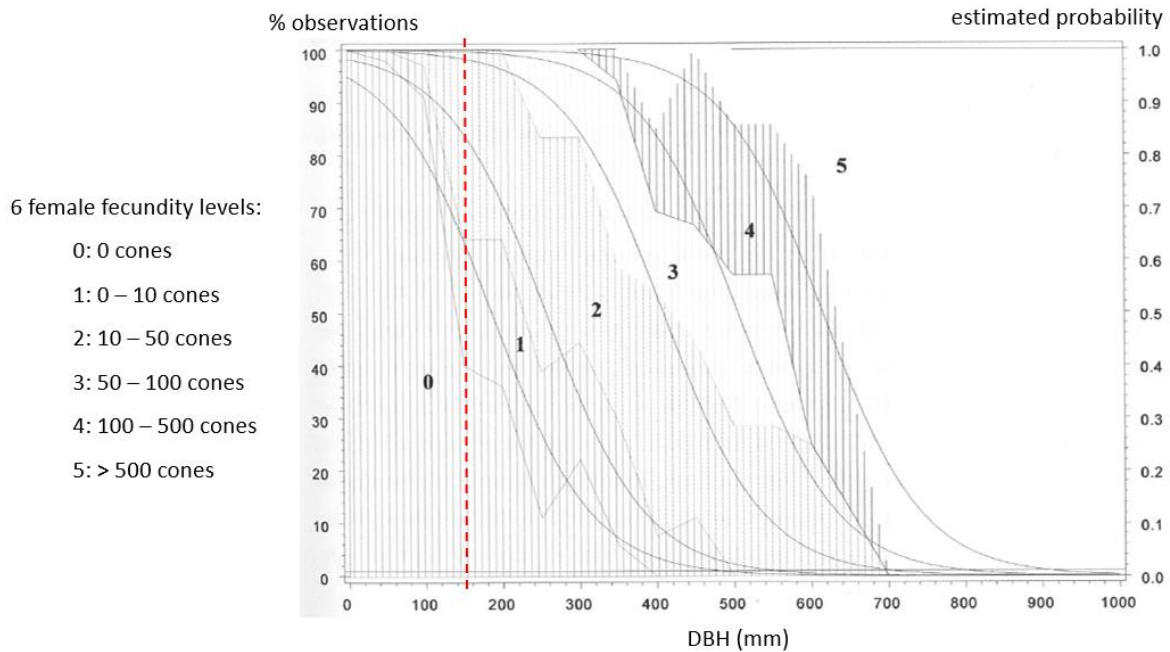


Figure 2. female fecundity as a function of DBH (regardless of crown height in this figure) in *C. atlantica*, observed data (hatching) and estimated probabilities (smooth lines) (Bertrand 2004). The red dotted line represents the sexual maturity threshold used in Luberon2, above this threshold the fecundity level is randomly drawn each year depending on tree DBH (e.g. a tree with DBH = 400mm will have higher probability to fall into level 2 or 3).

References

Bertrand A, 2004. Dynamique naturelle du Cèdre de l'Atlas (*Cedrus atlantica* Manetti) au Mont Ventoux. Approche spatio-temporelle et éléments de modélisation. DEA Aix-Marseille. https://capsis.cirad.fr/capsis/help_en/luberon2

Courbet F. 2002. Modélisation de la croissance et de la qualité du Cèdre : intégration des modèles dans Capsis. In : Rapport convention MAPA-DERF / INRA n° 61.45.47/01.
<https://hal.archives-ouvertes.fr/hal-03654591>

Perin J., Claessens H., Lejeune P., Brostaux Y., Hébert J., 2017. Distance-independent tree basal area growth models for Norway spruce, Douglas-fir and Japanese larch in Southern Belgium. *European Journal of Forest Research*, 136:193-204.
<https://doi.org/10.1007/s10342-016-1019-y>

Appendix 4 - Supplementary Figures

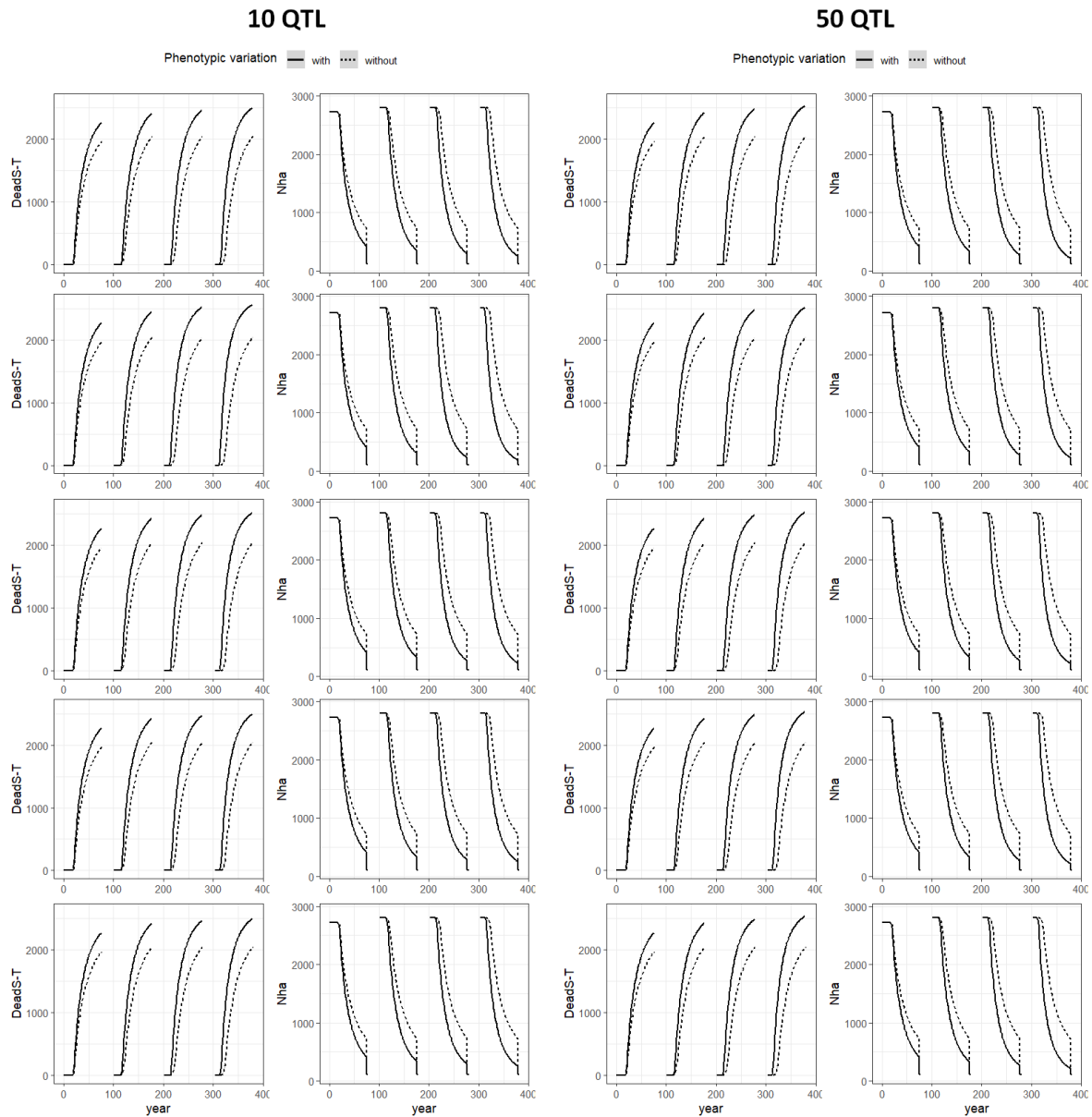


Figure S3. (Part 1) Dynamics of dendrometric and demographic variables in the long cycle scenario without thinning and without disturbance, with or without phenotypic variation (line types): number of deaths by self-thinning per hectare (*DeadS-T*) and number of trees per hectare (*Nha*). This figure illustrates all the genetic setups for 10 QTL ($n=5$) on the left and 50 QTL ($n=5$) on the right. The 95% interval over 10 replicates, represented by a shaded area, here is imperceptible. The pre-recruitment period is deliberately not represented because the genotype is not considered in the model during this phase.

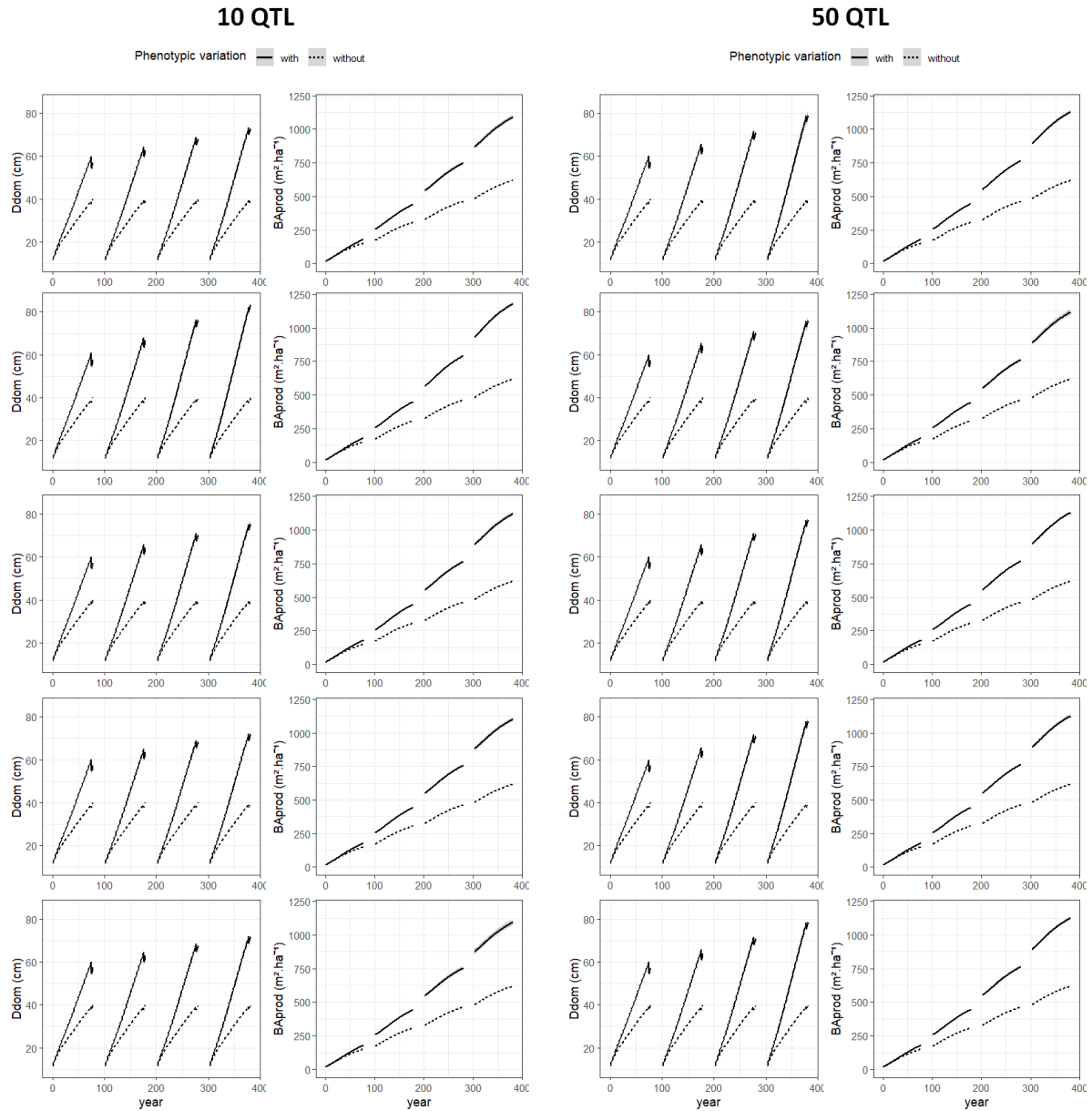


Figure S3. (Part 2) Dynamics of dendrometric and demographic variables in the long cycle scenario without thinning and without disturbance, with or without phenotypic variation (line types): dominant diameter (D_{dom}) and cumulated basal area production per hectare (BA_{prod}). This figure illustrates all the genetic setups for 10 QTL ($n=5$) on the left and 50 QTL ($n=5$) on the right. The 95% interval over 10 replicates, represented by a shaded area, here is imperceptible. The pre-recruitment period is deliberately not represented because the genotype is not considered in the model during this phase.

10 QTL

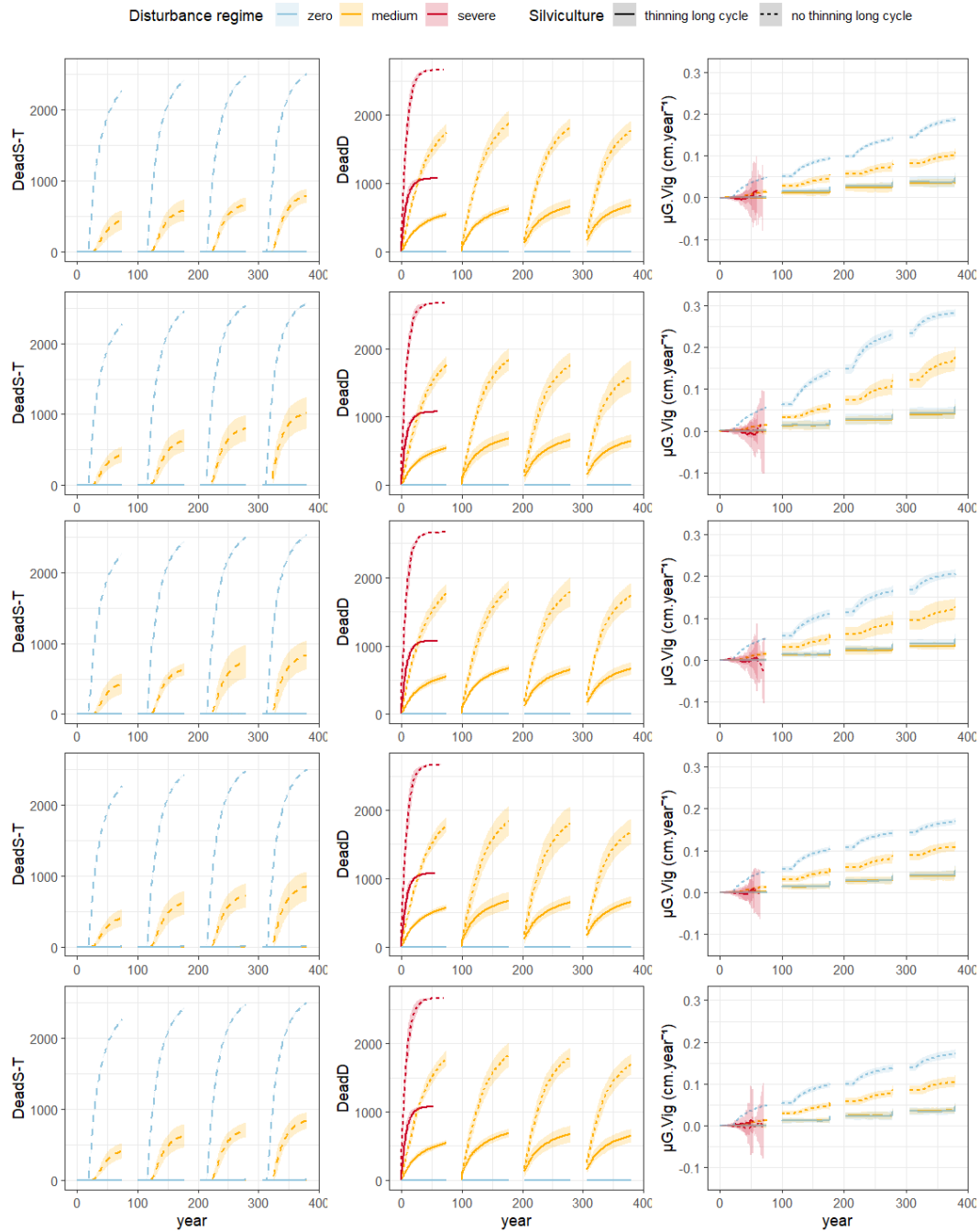


Figure S4. (Part 1) Dynamics of mortality and genetic changes in the long cycle scenarios with phenotypic variation, with or without thinnings (line types) and three disturbance regimes (colors): deaths by self-thinning ($DeadS-T$), deaths by disturbance ($DeadD$) and population genetic mean of vigor ($\mu G.Vig$). This figure illustrates all the genetic setups for 10 QTL ($n=5$); see part 2 for 50 QTL. The shaded areas represent the 95% intervals over 10 replicates for each scenario. With the severe disturbance regime, the population collapsed during the first cycle. Trees are 25-years old when simulations start at year 0. The pre-recruitment period is deliberately not represented because the phenotype is not considered in the model during this phase.

50 QTL

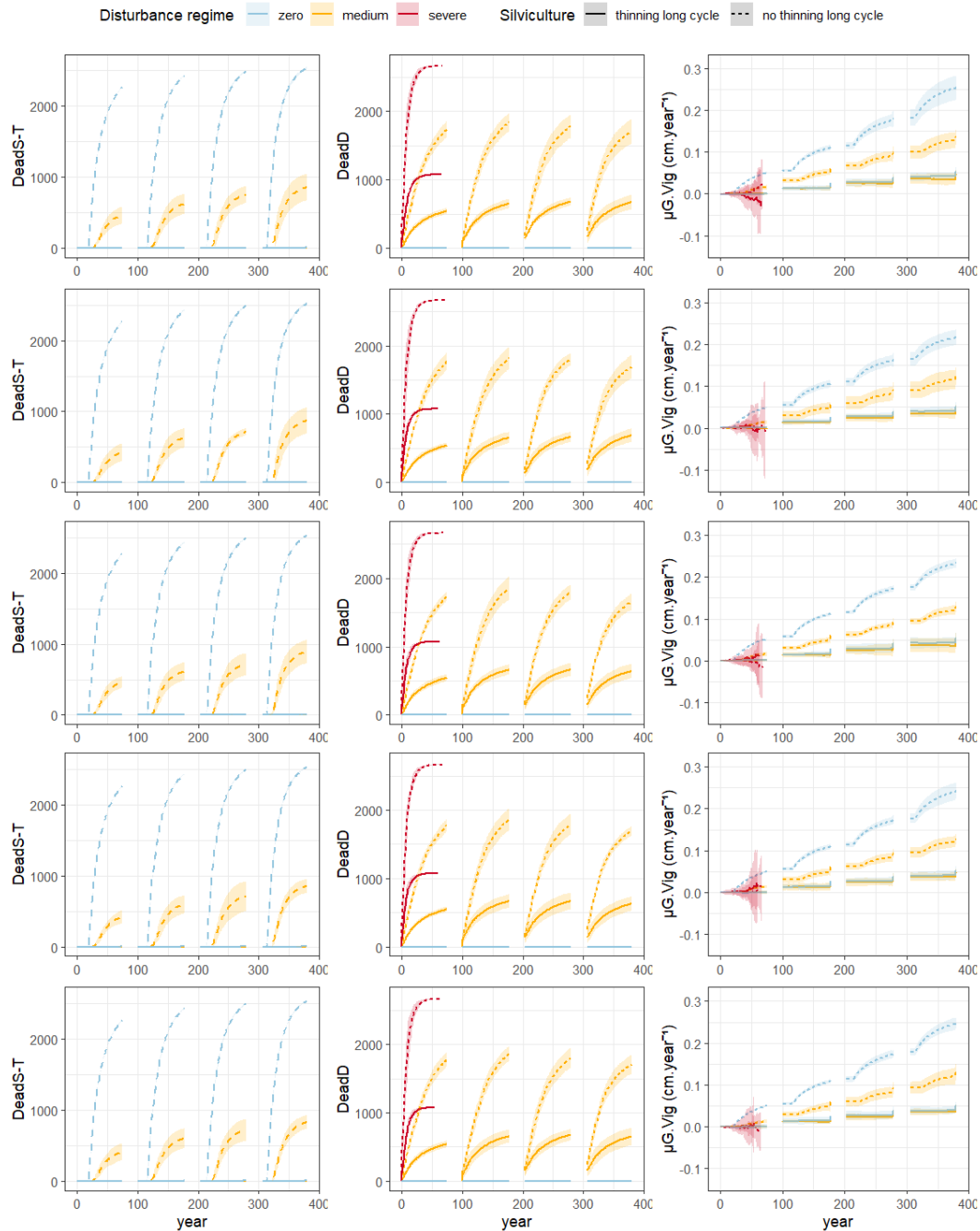


Figure S4. (Part 2) Figure S4. (Part 1) Dynamics of mortality and genetic changes in the long cycle scenarios with phenotypic variation, with or without thinnings (line types) and three disturbance regimes (colors): deaths by self-thinning (*DeadS-T*), deaths by disturbance (*DeadD*) and population genetic mean of vigor ($\mu G.Vig$). This figure illustrates all the genetic setups for 50 QTL ($n=5$); see part 2 for 10 QTL. The shaded areas represent the 95% intervals over 10 replicates for each scenario. With the severe disturbance regime, the population collapsed during the first cycle. Trees are 25-years old when simulations start at year 0. The pre-recruitment period is deliberately not represented because the phenotype is not considered in the model during this phase.

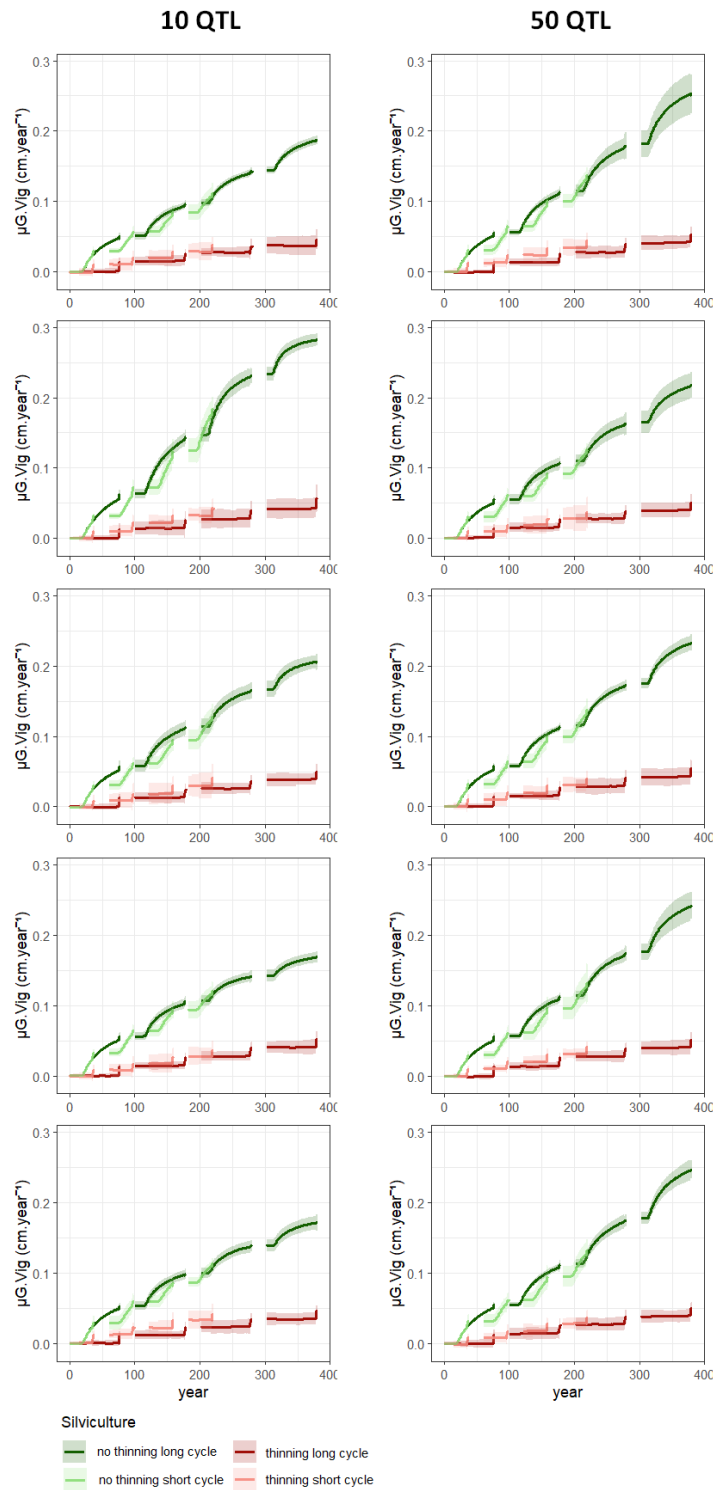


Figure S5. Dynamics of the population genetic mean of vigor ($\mu G.Vig$) in four scenarios, short and long cycle with or without thinnings (colors). This figure illustrates all the genetic setups for 10 QTL ($n=5$) on the left and 50 QTL ($n=5$) on the right. The shaded areas represent the 95% intervals over 10 replicates for each scenario. Trees are 25-years old when simulations start at year 0. The pre-recruitment period is deliberately not represented because the genotype is not considered in the model during this phase.

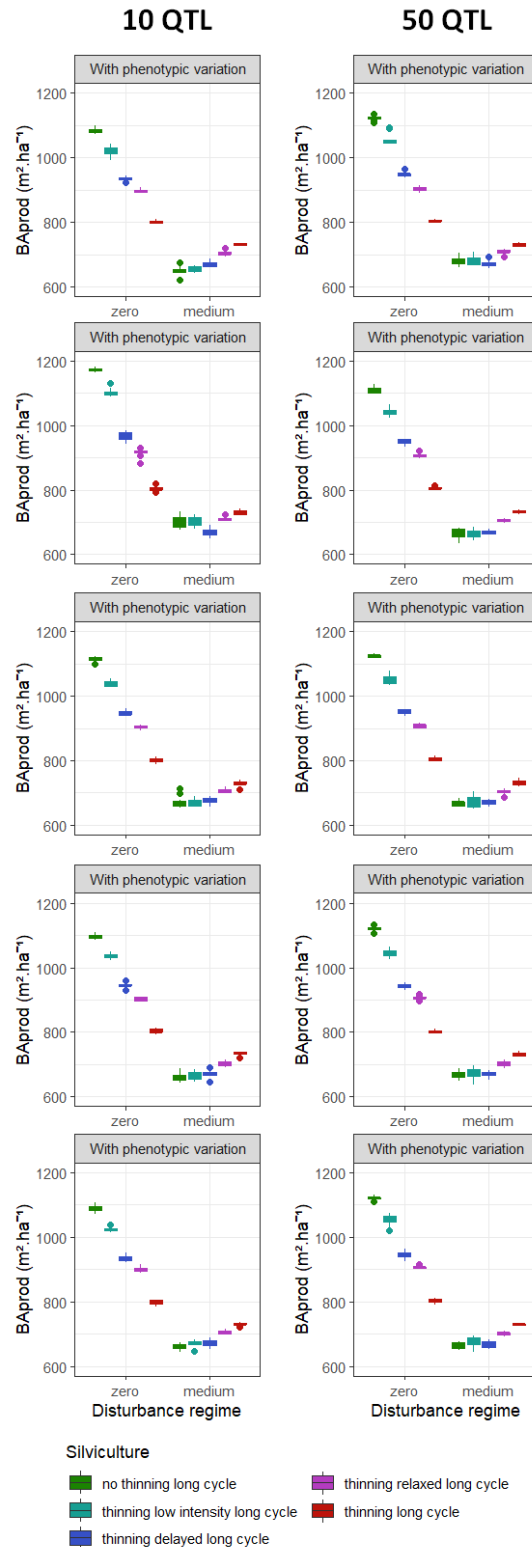


Figure S7. Basal area production (BAprod) at the end of the fourth silvicultural cycle in the long-cycle silvicultural scenarios (colors) and disturbance regimes (x-axes, the severe disturbance regime is not represented because it led to population collapse). This figure illustrates all the genetic setups for 10 QTL ($n=5$) on the left and 50 QTL ($n=5$) on the right. The boxplots illustrate the distribution of values over 10 replicates in each case.

Article 3. Données et Figures supplémentaires

Supplementary table 1. Soil parameters by soil types: humidity at field capacity (θ_{fc}), humidity at wilting point (θ_{wilt}), humidity at saturation (θ_{sat}), air-entry matric potential (Ψ_e), soil water retention parameter (b). θ_{fc} and θ_{wilt} were assessed for France forest soil using Baize & Jabiol 1995, while θ_{sat} , Ψ_e and b were assessed using Bonan, 2019.

Soil type	θ_{fc}	θ_{wilt}	θ_{sat}	$\Psi_e (10^{-4} \text{ MPa})$	b
Sandy clay loam	0.22	0.11	0.42	-29.24	7.12
Clay	0.37	0.25	0.451	-39.61	11.4
Silty clay	0.32	0.19	0.492	-47.92	10.4
Loam	0.38	0.25	0.451	-46.75	5.39
Sandy clay	0.33	0.22	0.426	-14.96	10.4
Clay loam	0.27	0.13	0.476	-61.61	8.52
Sandy clay silt	0.24	0.12	0.42	-29.24	7.12
Sandy loam	0.15	0.07	0.435	-21.32	4.90
Silt loam	0.23	0.1	0.485	-76.87	5.30
Loamy sand	0.19	0.09	0.41	-8.80	4.38
Sand	0.08	0.03	0.395	-11.83	4.05
Sandy clay	0.19	0.1	0.426	-14.96	10.4
Loamy sand	0.12	0.05	0.41	-8.80	4.38
Silt clay loam	0.17	0.08	0.477	-34.81	7.75

Supplementary table 2. CASTANEA parameters to simulate the drought stress level (*StressLvl*) for the five species studied (*Fagus sylvatica*, *Pseudotsuga menziesii*, *Pinus pinaster*, *Quercus petraea* and *Quercus robur*).

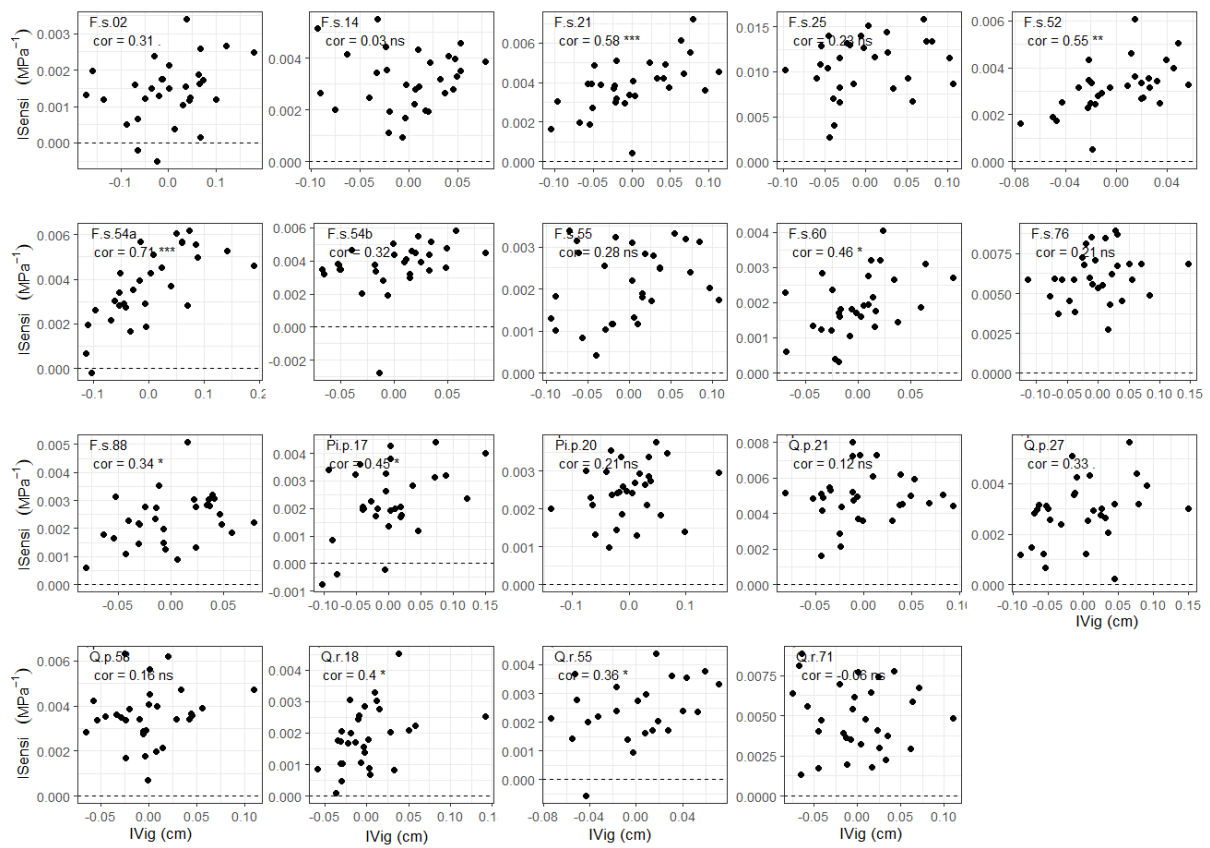
CASTANEA Parameter	<i>F. sylvatica</i>	<i>P. menziesii</i>	<i>P. pinaster</i>	<i>Q. petraea</i>	<i>Q. robur</i>
Nitrogen in leaves (%)	2.2	1.7	0.97	2.12	1.85
Leaf Mass per Area of sun leaves (g/m ²)	100	360	308	92	93
Wood reflectance in PIR domain	0.39	0.34	0.49	0.3	0.39
Wood reflectance in PAR domain	0.16	0.14	0.15	0.15	0.16
Leaf reflectance in PIR domain	0.359	0.263	0.287	0.332	0.332
Leaf transmittance in PIR domain	0.381	0.24	0.186	0.36	0.36
Leaf reflectance in PAR domain	0.085	0.096	0.093	0.095	0.095
Leaf transmittance in PAR domain	0.058	0.044	0.038	0.063	0.063
Water storage capacity per unit of leaf area (mm/m ²)	0.2	0.4	0.208	0.4	0.2
Water storage capacity per unit of bark area (mm/m ²)	0.3	0.32	1.95	0.8	0.3
Slope of the water interception coefficient	0.85	0.85	2.7	0.85	0.85
Intercept of the water interception coefficient	1.9	1.5	1.9	1.9	1.9
Ratio between stem flow and throughfall	0.35	0.35	0.35	0.35	0.35
Intercept of ball and berry relation	0.0017	0.000492	0.000451	0.0002829	0.0003034
Slope of ball and berry relation	11.8	9.5	8.594	9.5	9.27
Capacitance of trunk	0.04	0.04	0.04	0.04	0.04
Average soil resistance from soil to leaves	11465	15000	18000	11465	11465
Minimum midday leaf water potential (Mpa)	-2.37	-2.1	-2	-3.17	-3.2
Dependency between Vcmax and leaf nitrogen density	26	21.5	14.38	34.04	27
Base temperature for forcing budburst	0	1	1	4	3.5
Base temperature for leaf growth	0	0	0	0	11
Base temperature for forcing leaf fall	20	20	20	20	20
Date of onset of rest	60	10	10	40	40
Date of onset of ageing	213	213	213	213	213
Critical value of state of forcing (from quiescence to active period)	250	500	400	385	385
Critical value of state of forcing (from leaf development to maximum LAI)	200	350	350	200	200
Critical value of state of forcing (from leaf development to leaf maturity)	600	1000	1000	1000	424
Critical value of state of forcing (from nstart2 to leaf fall period)	225	100	100	230	100
Critical value of state of forcing from nstart2 to end of wood growth	100	300	300	100	100

Supplementary table 3. Characterization of the selected populations ($n = 22$) for the mixed model analysis (eq. 7.8). An abbreviated name was assigned to the populations according to the species and the number of the French department where they were sampled.

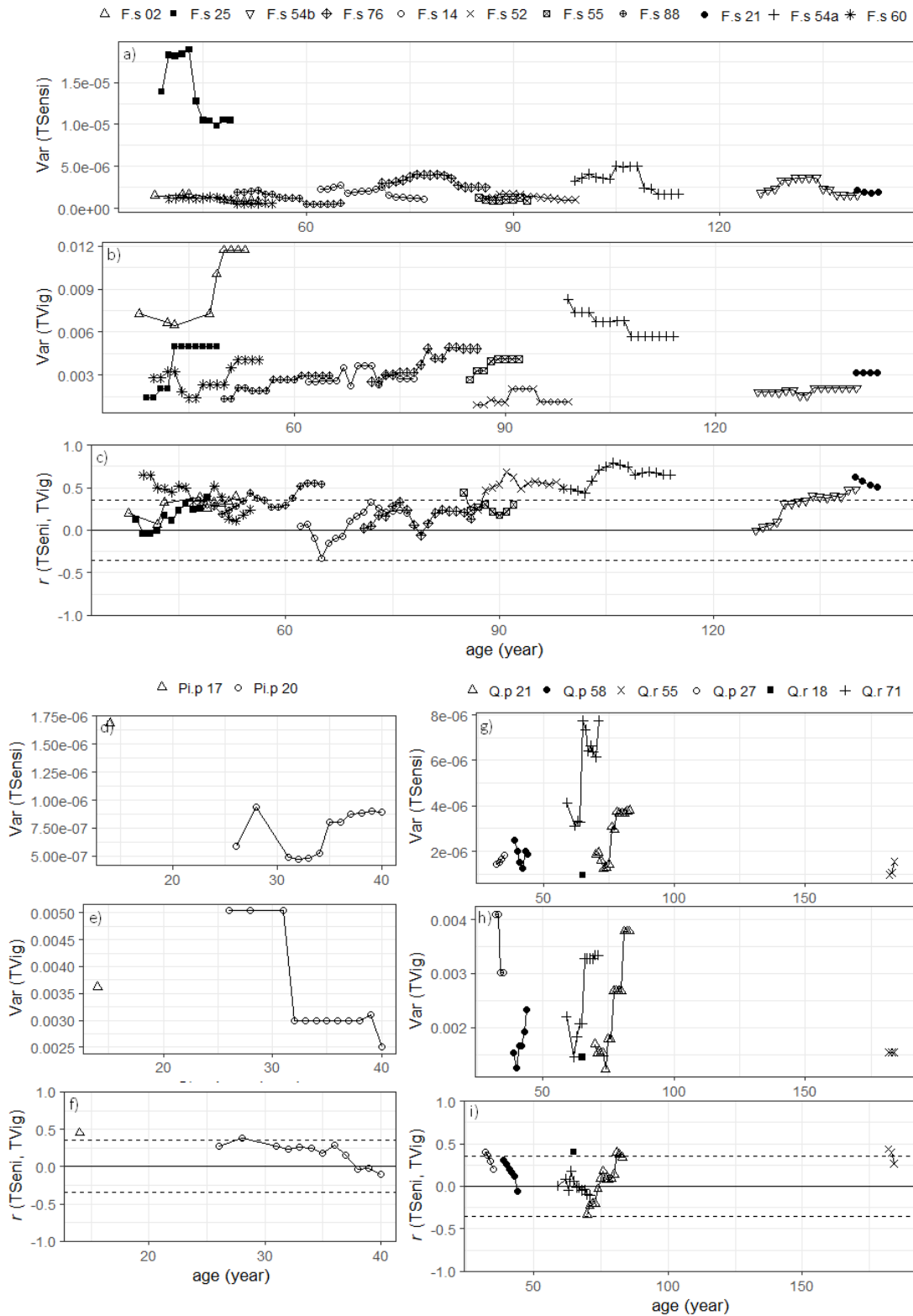
Population	Latitude	Longitude	Elevation (m)	Slope (°)	Precipitation (mm)		Mean Tmax (°C)		Mean Tmin (°C)	ESW (mm)	Nha	Age at sampling (year)	Average age in the selected intervals (year)
					Year	JJA	Year	JJA	year				
<i>F. sylvatica</i> (n=11)													
F.s. 02	49°12'21" N	3°07'36" E	145	0	703	167	13.6	22.7	6.6	151	336	63	47
F.s. 14	49°10'57" N	0°51'23" W	90	4	901	173	13.2	19.5	7.4	109	310	87	70
F.s. 21	47°48'50" N	4°51'18" E	400	3	885	211	13.2	22.2	6.0	19	298	153	142
F.s. 25	47°11'31" N	6°16'41" E	570	2	1402	347	11.9	20.3	5.7	148	857	59	44
F.s. 52	47°47'46" N	5°04'17" E	440	0	937	218	12.2	20.7	6.1	37	324	109	93
F.s. 54a	48°30'35" N	6°42'23" E	325	5	790	202	12.7	21.3	5.9	173	374	124	107
F.s. 54b	48°38'57" N	6°04'04" E	390	2	800	204	12.5	21.0	5.8	52	234	150	133
F.s. 55	49°10'15" N	5°00'17" E	250	0	656	215	13.4	20.9	6.6	121	214	102	89
F.s. 60	49°19'27" N	2°52'34" E	138	0	890	168	12.3	21.2	6.6	75	635	65	48
F.s. 76	49°42'39" N	1°19'34" E	210	0	1046	185	12.4	19.0	5.6	148	221	96	79
F.s. 88	48°06'21" N	6°14'50" E	400	3	940	254	12.9	20.9	6.7	107	766	75	57
mean	48°36'19"N	4°14'44"E	305	1.7	907	213	12.8	20.8	6.3	104	415	98	82
<i>P. menziesii</i> (n=3)													
Ps.m. 34	43°26'54" N	2°42'56" E	700	15	1408	162	13.7	21.8	8.0	49	305	49	32
Ps.m. 61	48°34'29" N	0°04'05" W	375	4	921	180	13.2	21.1	5.6	99	567	30	17
Ps.m. 69	45°56'51" N	4°28'42" E	520	50	1031	242	13.0	21.7	6.1	51	798	23	13
mean	45°59'25"N	2°22'31"E	532	23	1120	195	13.3	21.5	6.6	66	557	34	21
<i>P. pinaster</i> (n=2)													
Pi.p. 17	45°58'59" N	1°16'25" W	15	0	783	127	15.7	22.2	10.1	78	1600	23	13
Pi.p. 20	41°45'08" N	9°12'23" E	850	10	1422	116	13.0	20.0	9.2	91	1000	50	34
mean	43°52'04"N	5°14'24"E	433	5	1003	122	14.4	21.1	9.7	85	1300	37	24
<i>Q. petraea</i> (n=3)													
Q.p. 21	47°04'58" N	5°04'30" E	220	0	778	191	14.3	23.5	7.0	275	243	95	77
Q.p. 27	49°21'58" N	1°30'15" E	175	0	745	165	13.2	20.8	6.7	198	205	57	34
Q.p. 58	46°58'13" N	3°39'39" E	270	7	896	199	14.0	22.2	7.1	221	598	64	42
mean	47°48'23"N	3°24'48"E	222	2.3	806	185	13.9	22.2	6.9	232	349	72	51
<i>Q. robur</i> (n=3)													
Q.r. 18	46°49'33" N	2°34'27" E	175	2	756	179	14.5	22.8	7.0	147	763	90	65
Q.r. 55	49°01'21" N	5°46'01" E	220	0	866	198	13.0	21.4	6.3	85	65	207	183
Q.r. 71	46°58'13" N	5°14'36" E	190	0	770	189	14.5	23.7	7.1	273	265	84	66
mean	47°36'22"N	4°31'41"E	195	0.7	797	189	14.0	22.7	6.8	168	364	127	105

Supplementary table 4. Within- and between-population variances of sensitivity and vigor: within-population variances of sensitivity ($var(ISensi)$), within-species between-population variances of sensitivity ($var(\mu Sensi/sp)$), between-population variance of sensitivity ($var(\mu Sensi)$), within-population variances of vigor ($var(IVig)$), within-species between-population variances of vigor ($var(\mu Vig/sp)$), and between-population variance of vigor ($var(\mu Vig)$).

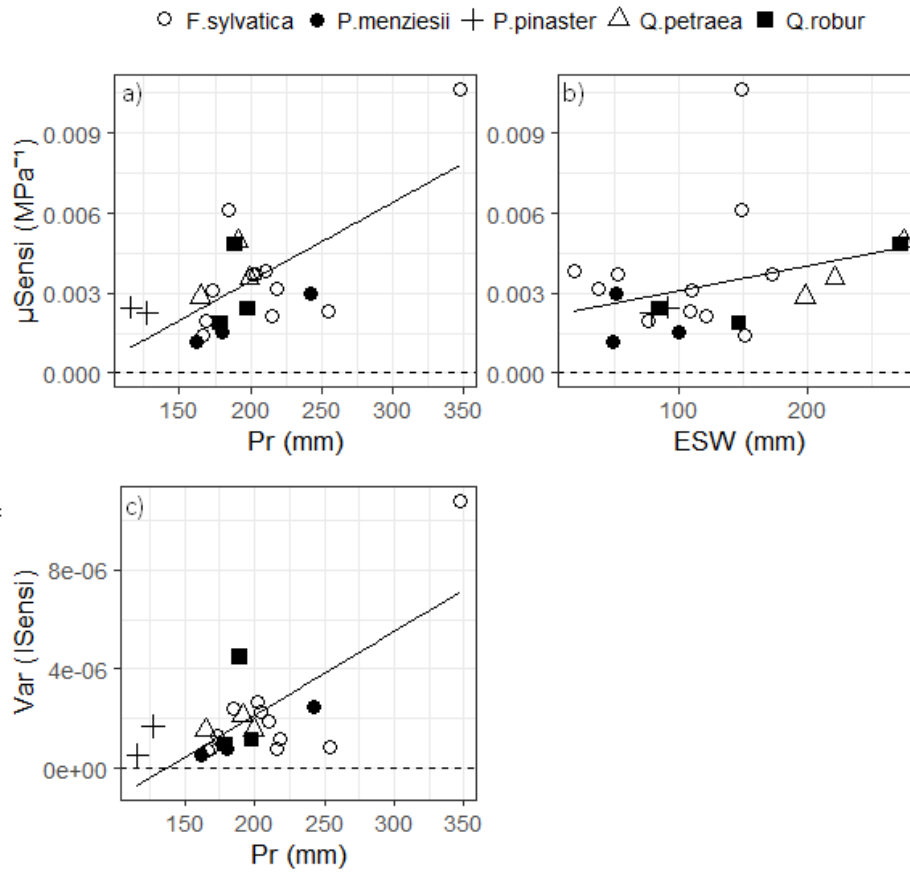
Population	$var(ISensi)$	$var(\mu Sensi/sp)$	$var(IVig)$	$var(\mu Vig/sp)$
<i>F. sylvatica</i> (n =11)		6.75×10^{-6}		3.66×10^{-3}
F.s. 02	7.33×10^{-7}		6.46×10^{-3}	
F.s. 14	1.30×10^{-6}		1.94×10^{-3}	
F.s. 21	1.87×10^{-6}		3.19×10^{-3}	
F.s. 25	1.08×10^{-5}		2.84×10^{-3}	
F.s. 52	1.20×10^{-6}		1.07×10^{-3}	
F.s. 54a	2.68×10^{-6}		5.54×10^{-3}	
F.s. 54b	2.30×10^{-6}		1.50×10^{-3}	
F.s. 55	7.60×10^{-7}		3.15×10^{-3}	
F.s. 60	7.55×10^{-7}		1.28×10^{-3}	
F.s. 76	2.43×10^{-6}		2.88×10^{-3}	
F.s. 88	8.47×10^{-7}		1.61×10^{-3}	
<i>P. menziesii</i> (n =3)		8.76×10^{-7}		6.10×10^{-3}
Ps.m. 34	5.01×10^{-7}		8.86×10^{-3}	
Ps.m. 61	7.86×10^{-7}		1.02×10^{-2}	
Ps.m. 69	2.47×10^{-6}		5.33×10^{-3}	
<i>P. pinaster</i> (n =2)		2.23×10^{-8}		4.56×10^{-3}
Pi.p. 17	1.69×10^{-6}		3.61×10^{-3}	
Pi.p. 20	5.23×10^{-7}		3.26×10^{-3}	
<i>Q. petraea</i> (n =3)		1.10×10^{-6}		1.21×10^{-3}
Q.p.21	2.01×10^{-6}		1.82×10^{-3}	
Q.p. 27	1.55×10^{-6}		3.34×10^{-3}	
Q.p. 58	1.56×10^{-6}		1.39×10^{-3}	
<i>Q. robur</i> (n =3)		2.48×10^{-6}		8.00×10^{-5}
Q.r. 18	9.39×10^{-7}		1.45×10^{-3}	
Q.r. 55	1.13×10^{-6}		1.54×10^{-3}	
Q.r. 71	4.49×10^{-6}		2.07×10^{-3}	
<i>All populations</i> (n =22)		$var(\mu Sensi)$ 4.20×10^{-6}		$var(\mu Vig)$ 1.97×10^{-2}



Supplementary figure 1. Correlation between intrinsic sensitivity ($ISensi$) and intrinsic vigor ($IVig$) in the *Fagus sylvatica* (F.s.), *Pinus pinaster* (Pi.p.), *Quercus petraea* (Q.p.) and *Quercus robur* (Q.r.) selected populations. Each point represents an individual tree. Among the nineteen populations, the correlation was significantly positive in eight populations at threshold 0.05 and in three populations at threshold 0.1. The significance level is indicated on the graphs by '***' at $p < 0.001$, '**' at $p < 0.01$, '*' at $p < 0.05$, '.' at $p < 0.1$ and 'ns' above. The dotted lines indicate zero sensitivity. Note that some trees were insensitive, i.e., $ISensi \leq 0$.



Supplementary figure 2. Variances (a, b, d, e, g, h) and correlation (c, f, i) of temporal sensitivity (*TSensi*) and temporal vigor (*TVig*) for each interval T of the *Fagus sylvatica* (F.s.; a, b, c), *Pinus pinaster* (Pi.p.; d, e, f), *Quercus petraea* and *Quercus robur* (respectively Q.p. and Q.r.; g, h, i) selected populations. Each point represents an interval T characterized by the average age of the trees in the population (*age*). On the graphs c, f and i, the dashed lines represent the values beyond which correlation coefficients are significant at $p < 0.05$ computed for a sample size of $n = 30$ individuals.



Supplementary figure 3. Effects of environmental factors that significantly impacted average population sensitivity (μSensi ; a, b) and within-population variance of sensitivity ($\text{var} (ISensi)$; c), i.e., average summer precipitations (Pr) and extractable soil water (ESW). Each point represents a population. The lines shown are the regression coefficients on all the selected populations ($n = 22$): $\mu\text{Sensi} = -3.56 \times 10^{-3} + 2.94 \times 10^{-5} Pr + 9.17 \times 10^{-6} ESW$ ($R^2 = 0.56$); $\text{var} (ISensi) = -4.63 \times 10^{-6} + 3.38 \times 10^{-8} Pr$ ($R^2 = 0.53$).

Article 4. Calibration de trois distributions gamma du niveau de stress (A) et Figures supplémentaires (B)

Appendix A. Calibration of three stressLevel Gamma distributions

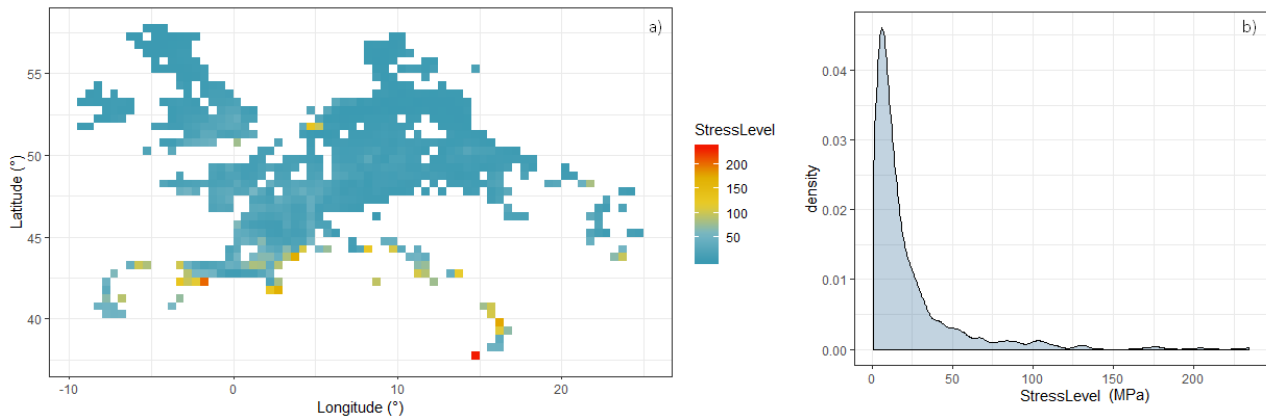
Our objective was to calibrate three water stress level Gamma distributions modulated by the stand leaf area index (LAI). We performed all the following analyses with R version 3.6.2.

CASTANEA simulation plan

The aggregation of European pedoclimatic data produced by Petit-Cailleux et al. (2021) corresponds to 3,411 raster cells with a spatial resolution of 0.5° by 0.5°. Of these cells, 698 contained at least one reported stand of Douglas-fir (Mauri et al. 2017). Daily climate data are available from 1979 to 2008. In each of the 698 Douglas-fir raster cells, we performed nine CASTANEA (Dufrêne et al., 2005; Davi & Cailleret 2017) simulations by varying the LAI forcing value between 2 and 10, which corresponds to the LAI range generally observed in naturally regenerating Douglas-fir stands (Smith et al. 1993). As output, we focused on an annual water stress level indicator, the *stressLevel* (Fririon et al., 2023), which integrates the annual soil water balance like a Palmer index does. As a sum of water potential, the *stressLevel* is systematically negative. Constrained by the Gamma distribution calibration algorithms, in the following, we use the absolute values of *stressLevel*, which also goes in the most logical direction: a high positive value of *stressLevel* corresponds to high stress.

Data overview and selection of three *stressLevel* regimes

Douglas-fir is mainly found in France, Germany, the British Isles, Italy (in the Apennines), the Czech Republic, Belgium, the Netherlands and Denmark, and marginal populations are found as far as the Highlands of Scotland, the slopes of Etna in Sicily, the mountains of Portugal, the plains of Poland, and the Carpathians (Supp. Fig. A1). To characterise each raster cell, we computed the average *stressLevel* over all years and LAI values. We thus observed a wide range of water stress conditions, the average *stressLevel* over the European range of the Douglas-fir ranging from 1 to 234 MPa with a median of 11 MPa (Supp. Fig. A1). The raster cells with the highest average *stressLevel* correspond to Southern Europe while the average *stressLevel* remains low overall in the rest of Europe.

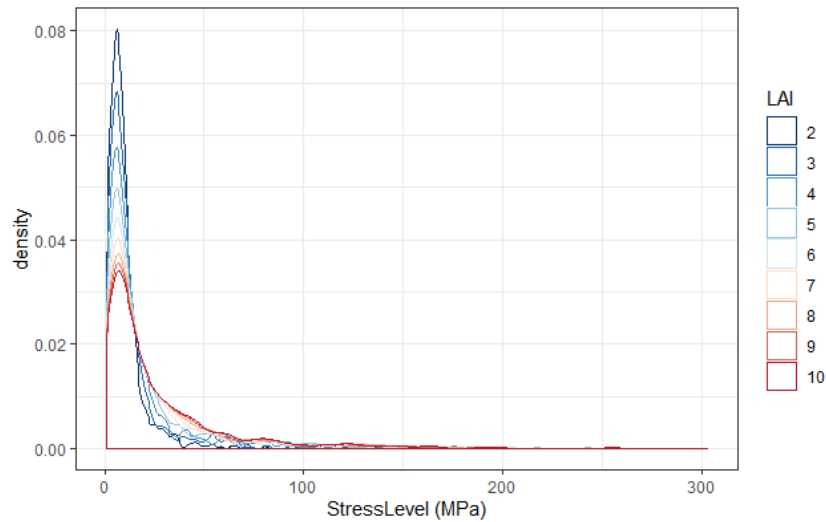


Supplementary figure A1. The average *stressLevel* over years and LAI values in the European range of Douglas-fir: (a) geographical distribution and (b) global density.

Based on the average *stressLevel*, we selected three stress regimes representative of the range observed in the European range of the Douglas-fir. First, we selected a zero-stress regime. Second, we intended to select the most intense stress regime observed. However, in *Luberon2*, we assumed a monotonic relationship between LAI and the shape and scale parameters of the Gamma distribution (see main text eq. 1,2), which was not the case for the two stress regimes with highest average *stressLevel* (data not shown). We thus retained the stress regime with the third highest *stressLevel* (179 MPa) as the intense stress regime. Third, we selected a medium regime with an average *stressLevel* approximately 2.5 times lower than the intense stress regime (69 MPa). Preliminary simulation with *Luberon2* showed that the intense stress regime severely reduces tree growth and frequently leads to mortality, whereas the medium stress regime affects tree growth but very little survival.

Overall effect of LAI on *stressLevel*

To observe the overall effect of LAI on water stress, for each raster cell, we computed an average *stressLevel* over years for each value of LAI. As expected, higher LAI values accentuate the water stress level: *stressLevel* varied from 1 to 116 MPa for a LAI of 2 and from 1 to 299 MPa for an LAI of 10 (Supp. Fig. A2). When the climatic stress is always low or zero, the LAI has no effect on *stressLevel*, resulting in a large number of raster cells with a very low average *stressLevel* even for a LAI of 10.



Supplementary figure A2. Distribution of average *stressLevel* over years for each LAI value.

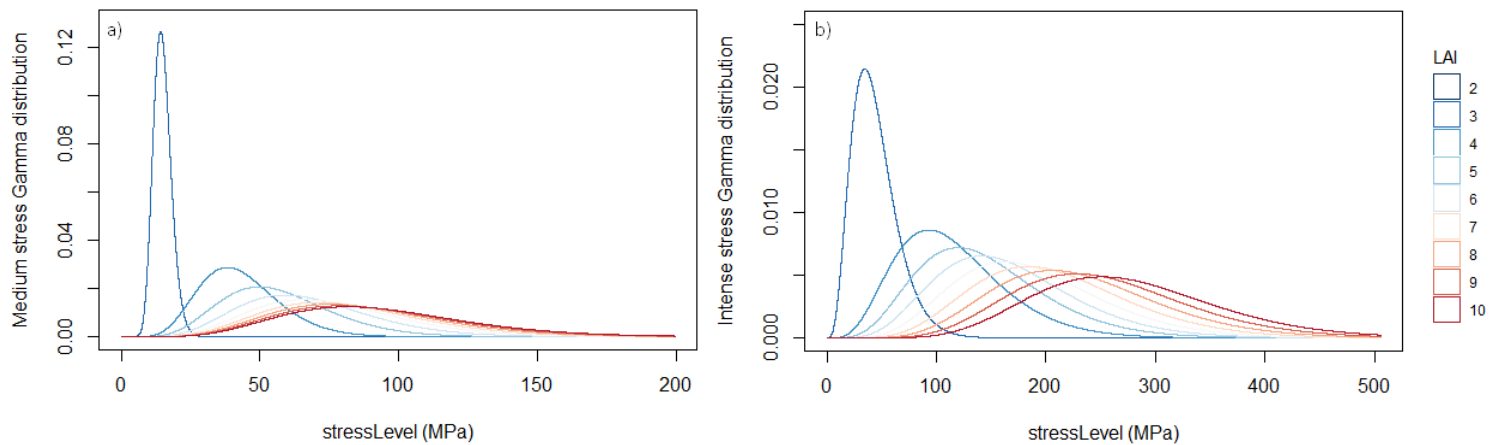
Calibration process for the three selected *stressLevel* Gamma distributions

The zero-stress regime does not require calibration because it corresponds to deactivating the disturbance in the simulations. For the intense and medium stress regimes, we determined the parameters a_{shape} , b_{shape} , c_{shape} , a_{scale} , b_{scale} and c_{scale} (main text eq. 1,2) using nonlinear regression with the `nls {stat}` R function. Supplementary Table A1 gives the fitted value of the six parameters. Regarding the medium stress regime, the R^2 was 0.98 for the relation between the scale and LAI and 0.99 for the relation between the shape and LAI. Regarding the intense stress regime, the R^2 was 0.85 for the relation between the scale and LAI and 0.92 for the relation between the shape and LAI.

Supplementary table A1. The six parameters of the selected *stressLevel* Gamma distributions fitted by nonlinear regression. For the zero stress regime, the disturbances are deactivated in the corresponding simulations.

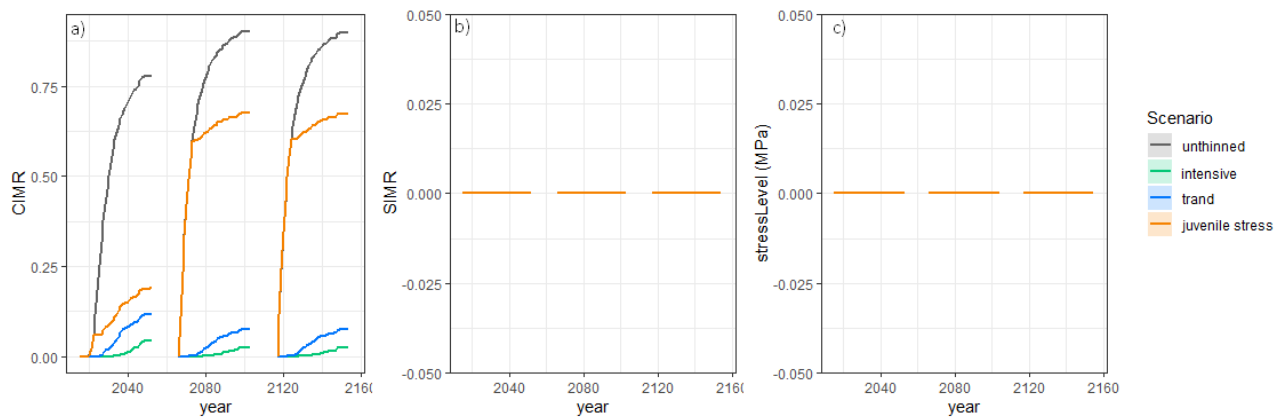
Distribution	aScale	bScale	cScale	aShape	bShape	cShape
<i>Medium stress</i>	-27.9	-0.7	17.9	1001.6	-6.2	7.6
<i>High stress</i>	-189.0	-3.5	26.3	0.3	1.3	3.7

As expected, the LAI strongly modulates the water stress level for both the intense and medium stress regimes (Supp. Fig. A3), the larger the LAI, the higher the *stressLevel*, on average. In addition, the higher the LAI, the higher the interannual variation of *stressLevel*. The larger the LAI, the less a change in these corresponds to a change in the *stressLevel* Gamma distribution.

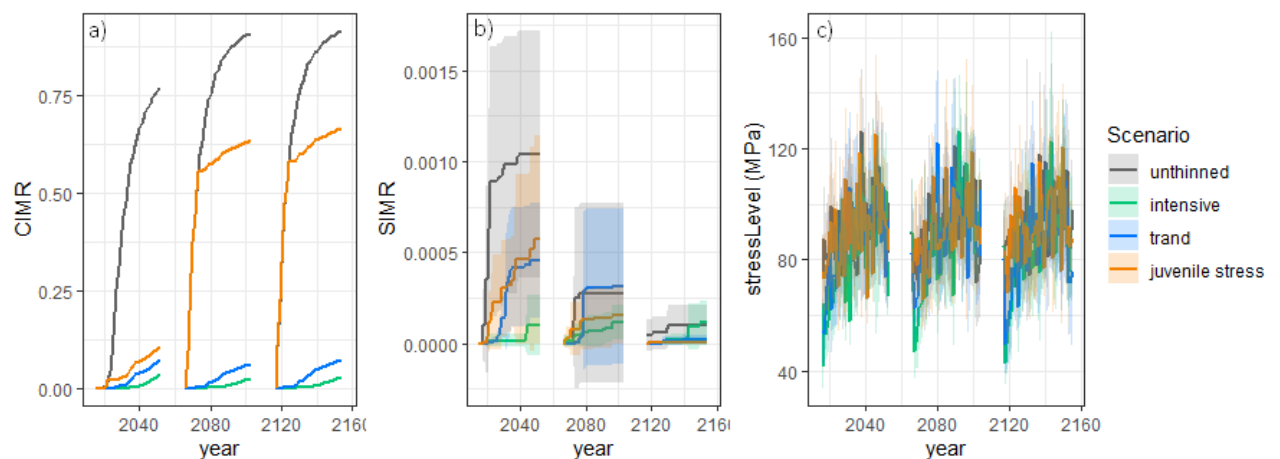


Supplementary figure A3. The *stressLevel* Gamma distributions modulated by the LAI to generate (a) the medium stress regime and (b) the intensive stress régime. The zero stress is not represented since the *stressLevel* is always 0.

Appendix B. Supplementary Figures



Supplementary Figure B1. Impact of the silvicultural scenario on the competition-induced mortality rate per silvicultural cycle (a), the stress-induced mortality rate per silvicultural cycle (b), and the stress level during three silvicultural cycles with zero disturbance regime and reference genetic variance. The four scenarios are represented by the colours: grey for the unthinned scenario, green for the trend, blue for the dynamic and orange for the juvenile stress. The shaded area represents the 95% probability interval around the mean of 10 replicates. The pre-recruitment period is deliberately absent because it constitutes a modelling artifice.



Supplementary Figure B2. Impact of the silvicultural scenario on the competition-induced mortality rate per silvicultural cycle (a), the stress-induced mortality rate per silvicultural cycle (b), and the stress level during three silvicultural cycles with medium disturbance regime and reference genetic variance. The four scenarios are represented by the colours: grey for the unthinned scenario, green for the trend, blue for the dynamic and orange for the juvenile stress. The shaded area represents the 95% probability interval around the mean of 10 replicates. The pre-recruitment period is deliberately absent because it constitutes a modelling artifice.

Annexe 2 : ressources pour le développement de Luberon2

Outil de travail pour implémenter le sapin Douglas (depuis Gymnos) et le formalisme de régimes d'impact sécheresse dans Luberon2

Le tableau comparatif entre les modèles Luberon2 et Gymnos ci-dessous a permis de caractériser les fonctions de dynamique et de croissance forestière des deux modèles afin de penser leur compatibilité pour intégrer le sapin Douglas dans Luberon2 et de penser l'intégration du formalisme de régime d'impact sécheresse.

Processus général	Méthode / Étape	Luberon2	Gymnos	Point de développement (>) et remarque (*)
Plusieurs espèces au sein du modèle	<i>Une structure adaptée à plusieurs espèces</i>	Le modèle d'origine est structuré et calibré pour une seule espèce : le cèdre.	<ul style="list-style-type: none"> La classe <code>GymnoSpecies</code> de type énumération (enum) contient la plupart des paramètres spécifiques aux espèces pour un modèle de dynamique commun (croissance et mortalité). Les classes <code>GymnoInitialParameters</code>, <code>GymnoInventoryLoader</code> et <code>GymnoStand</code> ont pour attribut <code>GymnoSpecies</code>. 	<p>> Restructurer Luberon2 pour ajouter la possibilité de simuler des peuplements monospécifiques de différentes espèces</p> <p>> Ajouter une fiche espèce spécifiant la valeur des variables espèces-dépendants</p>
Boucle d'évolution de pas de temps annuelle	<i>Exécuter une étape annuelle de la boucle d'évolution</i>	<p>Lub2Model.processEvolution</p> <ul style="list-style-type: none"> Crée de la <code>newScene</code> par copie partielle (<code>Lub2Scene.getEvolutionBase</code>) Pour chaque unité de croissance de chaque parcelle, exécute l'évolution (croissance et mortalité des arbres) (<code>Lub2Model.process[...]Evolution¹</code>) : <ul style="list-style-type: none"> Fait pousser tous les arbres en diamètre (<code>process[...]DiameterGrowth¹²</code>) Fait pousser la hauteur dominante (<code>HDom</code>) à partir du <code>HDom</code> précédent plus la croissance de <code>HDom</code> attendue de par l'âge du peuplement (<code>Lub2Utilities.calculateAnnualGrowthInHDom</code>) Màj l'âge de l'unité de croissance et de la moyenne quadratique des diamètres (<code>Dg</code>) Pour chaque arbre : calcule la nouvelle hauteur (<code>Lub2Utilities.calculateHeight</code>) et de la hauteur de base de houppier (<code>Lub2Utilities.calculateCrownBaseHeight</code>) par allométrie Màj le volume (<code>Vha</code>) et la surface terrière (<code>Gha</code>) de l'unité de croissance et calcul <code>prodVha</code> et <code>prodGha</code> avant mortalité Uniquement pour les <code>MainParcel</code>: dans chaque pixel, si la régénération a atteint l'âge de recrutement, supprime les arbres adultes du pixel (<code>processPixelRecruitmentManagement</code>) Processus de mortalité par auto-éclaircie (<code>Lub2Model.process[...]Mortality¹</code>) Màj les variables dynamiques de l'unité de croissance (<code>Dg</code>, <code>Ddom</code>, <code>Hdom</code>, <code>Gha</code>, <code>Vha</code>, <code>Nha</code>, ...) paramètres du modèle de croissance) (<code>Lub2Utilities.calculateDynamicCharacteristics</code>) * <ul style="list-style-type: none"> Impacts due aux perturbations (uniquement mortalité sécheresse pour le moment) (<code>Lub2Disturbances.execute</code>) Exécute la régénération si activée (<code>Lub2Model.runRegeneration</code>) 	<p>GymoModel.processEvolution</p> <ul style="list-style-type: none"> Crée de la <code>newScene</code> par copie partielle de la scène de référence (<code>GymnoStand.getEvolutionBase</code>) ; màj l'âge du peuplement (+1) Fait pousser tous les arbres en diamètre et en hauteur (<code>GymnoTree.processGrowth</code>), et les ajoute dans la <code>newScene</code> Màj des variables peuplement de la nouvelle scène après croissance (<code>nTree</code>, <code>cg</code>, <code>Hdom</code>, <code>SI</code>, <code>DHdom</code>, <code>Rdi</code>, ...) via <code>GymnoStand.calcStand</code> Processus de mortalité (<code>GymnoModel.runMortality</code>) Processus de décomposition (<code>runDecaying</code>) : place les arbres morts dans une autre collection Màj des variables peuplement de la nouvelle scène après mortalité (<code>GymnoStand.calcStand</code>) Exécute les dégâts liés aux cerfs (<code>GymnoModele.runNewBarkPeeling</code> et <code>GymnoModele.updateOldBarkPeelingDamage</code>) 	<p>> Ajouter un mode "script"</p> <p>* <code>Lub2Utilities.calculateDynamicCharacteristics</code> est également utilisé pour màj les variables dynamiques peuplement lors de l'initialisation du modèle (<code>Lub2Model.initializeModel</code>), à la fin de la régénération (<code>Lub2Model.runRegeneration</code>) et lors de l'étape de poste exécution (<code>Lub2Model.processPostIntervention</code>)</p>

Processus général	Méthode / Étape	Luberon2	Gymnos	Point de développement (>) et remarque (*)
Croissance des arbres en diamètre	Exécuter la croissance individuelle en diamètre (et en hauteur dans Gymnos)	<p>Lub2Model.process[...].DiameterGrowth¹ Pour chaque arbre de <i>Dbh</i> donné au sein d'une même unité de croissance aux paramètres de croissances (<i>diameterGrowthThreshold</i> et <i>alpha</i>) données :</p> <ul style="list-style-type: none"> Màj l'âge de l'arbre (<i>age + 1</i>) Si l'arbre est adulte (supérieur à l'âge de recrutement), màj son diamètre par la méthode <code>Lub2Utilities.calculateFutureDiameter</code> : <ul style="list-style-type: none"> Calcule l'accroissement en surface terrière (<i>dG</i>) de l'arbre en fonction de son <i>Dbh</i> initial, des paramètres du modèle de croissance de son unité de croissance que sont la pente <i>alpha</i> et le seuil <i>diameterGrowthThreshold</i> et d'une valeur phénotypique individuelle de vigueur (<i>phenoValue</i>) : $dG = \alpha \times (\pi \times Dbh - diameterGrowthThreshold) + phenoValue$ Si le <i>dG</i> calculé est négatif, retourne le <i>Dbh</i> initial de l'arbre Sinon, calcule le nouveau <i>Dbh</i> de l'arbre (<i>newDiam</i>) en fonction de <i>dG</i> et du <i>Dbh</i> initial retourne <i>newDiam</i> <p>• Si l'arbre dépasse pour la première fois le diamètre de fertilité, màj la date de première fructification (<i>setFirstFlow</i>)</p>	<p>GymnoTree.processGrowth Pour chaque arbre de circonférence (<i>circ</i>) donnée dans un peuplement de hauteur dominante (<i>HDom</i>), croissance en hauteur dominante (<i>DHDom</i>) et surface terrière (<i>BasalArea</i>) données :</p> <ul style="list-style-type: none"> Calcule le paramètre de croissance « seuil » : $A = aa \times HDom^{ab}$; <i>aa</i> et <i>ab</i> sont deux constantes spécifiques à l'espèce Calcule le paramètre de croissance « pente » : $P = pa + pb \times DHDom$; <i>pa</i> et <i>pb</i> sont deux constantes spécifiques à l'espèce Calcule le paramètre de croissance « souplesse du seuil »** : $m = 1 + exp((ma \times HDom - mb \times BasalArea))$; <i>ma</i> et <i>mb</i> sont deux constantes spécifiques à l'espèce Calcule la croissance en surface terrière : $Ig = 0.5 \times P \times (circ - m \times A + sqrt((m \times A + circ)^2 - 4 \times A \times circ))$ Calcule la croissance en circonférence**** : $dCirc = sqrt(circ^2 + Ig \times 4 \times \pi) - circ$ Calcule la croissance en diamètre : $dD = dCirc / \pi$ Calcule la croissance en hauteur : $dH = 0.799 \times DHDom \times atan(tan(1/0.799) \times (circ / CDom))$**** Fait grandir, màj l'âge et retourne le nouvel arbre 	<p>> Dans Luberon2, le modèle de croissance est à deux paramètres (<i>alpha</i> et <i>diameterGrowthThreshold</i>), alors que dans Gymnos il est à trois paramètres (<i>P</i>, <i>A</i> et <i>m</i>). Pour obtenir un modèle commun aux deux espèces : remplacer la méthode de Luberon2 par celle de Gymnos et fixer le paramètre <i>m</i> à 1 pour le cèdre</p> <p>* La valeur individuelle <i>phenoValue</i> est égale à <code>GeneticTree.getPhenoValue("diameterGrowth_cm")</code>, qui est directement appelé dans les arguments de la méthode <code>Lub2Utilities.calculateFutureDiameter</code>. Il est décrit dans la partie rose « Valeurs individuelles génétiques / phénotypiques ».</p> <p>** Contrairement à Luberon2, le modèle de croissance en diamètre de Gymnos est à 3 paramètres. S'ajoute aux deux premiers paramètres le paramètre « souplesse du seuil », qui devra être fixé à 1 pour le cèdre.</p> <p>*** Si la hauteur dominante du peuplement est en dessous de la gamme de validité (seuil <i>sc1</i> spécifique à l'espèce), alors la croissance en circonférence est calculée comme lors de la création d'un peuplement virtuel (voir <code>GymnoModel.createVirtualStand</code>).</p> <p>**** Attention, dans Gymnos la croissance en diamètre et la croissance en hauteur des arbres sont incluses dans une même méthode (<code>GymnoTree.processGrowth</code>).</p>
Croissance des arbres en hauteur	Calculer la croissance en hauteur dominante du peuplement (<i>AnnualGrowthInHDom</i> vs <i>DHDom</i>)	<p>Lub2Utilities.calculateAnnualGrowthInHDom</p> <ul style="list-style-type: none"> Retourne la croissance en hauteur dominante calculée en fonction de l'âge de l'unité de croissance et de la fertilité de la parcelle : $AnnualGrowthInHDom = calculateHDomAccordingAge[age + 1] - calculateHDomAccordingAge[age]$ 	<p>GymnoStand.calcDHDom appelé dans <code>GymnoStand.calcStand</code></p> <ul style="list-style-type: none"> Retourne le <i>DHDom</i> calculé comme la différence entre (1) le <i>HDom</i> attendu l'année suivante connaissant l'âge et le niveau de productivité du peuplement (<code>GymnoSpecies.calcHDom</code>) et (2) le <i>HDom</i> actuel : $DHDom = calcHDom[age + 1] - HDom[actuel]$ 	
	Calculer la hauteur dominante en fonction de l'âge et de la fertilité / la productivité du peuplement	<p>Lub2Utilities.calculateHDomAccordingAge</p> <ul style="list-style-type: none"> Calcule la hauteur dominante connaissant l'âge de l'unité de croissance et la fertilité de la parcelle formalisée comme l'asymptote de la relation <i>âge - HDom</i> : $Hdom = asymptote \times \left(1 - exp\left(\frac{-age}{c}\right)^{\frac{a}{asymptote^a + b}}\right)$, avec <i>a</i>, <i>b</i>, <i>c</i> et <i>d</i> des constantes Retourne <i>HDom</i> 	<p>GymnoSpecies.calcHDom**</p> <ul style="list-style-type: none"> Calcule le paramètre "niveau de productivité du peuplement" (<i>bi</i>) en connaissant un couple <i>Hdom - ageHdom</i> connu (<code>GymnoSpecies.calcHDomParameterBi</code>) : $bi = \frac{Hdom}{[1 - exp(-\frac{ageHdom}{c})]^r} - a \times ageHdom$, avec <i>a</i>, <i>c</i> et <i>r</i> des constantes spécifiques à l'espèce Calcule <i>Hdom</i> pour un âge donné en fonction de <i>bi</i> (<code>GymnoSpecies.calcHDomFromBi</code>) : $Hdom = (a \times age + bi) \times [1 - exp(-\frac{age}{c})]^r$, avec <i>a</i>, <i>c</i> et <i>r</i> des constantes spécifiques à l'espèce Retourne <i>Hdom</i> 	<p>* Dans Luberon2, le calcul de l'asymptote de la relation <i>âge - HDom</i> est effectué à partir d'un couple <i>Hdom - ageHdom</i> par la méthode <code>Lub2Utilities.calculateAsymptoteOfCurveHdomFunctionOfAge</code> qui est exécutée pour chaque parcelle lors de l'initialisation du modèle (<code>Lub2Modele.initializeModel</code>).</p> <p>** fonction non asymptotiques pour le sapin Douglas</p>
	Calculer la croissance en hauteur des arbres individuels	<p>Lub2Utilities.calculateHeight</p> <ul style="list-style-type: none"> Màj la hauteur de chaque arbre en fonction de leur <i>Dbh</i>, de la hauteur dominante (<i>HDom</i>) et du diamètre dominant (<i>Ddom</i>) (<code>Lub2Utilities.calculateDdomFromTreeCollection</code>) : $hauteur = 1,3 + (Hdom - 1,3) \times \frac{(1 - exp(-0.017 \times diameter \times \pi))}{(1 - exp(-0.017 \times Ddom \times \pi))}$ 	Inclus dans <code>GymnoTree.processGrowth</code>	<p>* Si l'utilisateur choisit la taille de pixel recommandée de 15m x 15m, <i>Ddom</i> est égal au <i>Dbh</i> du plus gros arbre de l'unité de croissance.</p>

Processus général	Méthode / Étape	Luberon2	Gymnos	Point de développement (>) et remarque (*)
Mise à jour des caractéristiques dynamiques du peuplement	Mettre à jour les caractéristiques dynamiques du peuplement, en particulier les paramètres du modèle de croissance	<p>Lub2Utilities.calculateDynamicCharacteristics</p> <ul style="list-style-type: none"> • Mäj <i>Gha</i> (Lub2Utilities.calculateGha[$\sum Dbh_i$]), <i>Vha</i> (Lub2Utilities.calculateVha[$\sum Dbh_i$, $\sum hauteur_i$]) et <i>Nha</i> • Mäj les variables de la scène dominante : <i>Dg</i>, <i>Ddom</i> (Lub2Utilities.calculateDdomFromTreeCollection / = Dg) *, <i>Hdom</i> (Lub2Utilities.calculateHeight [Ddom]) **, <i>CBHdom</i> (Lub2Utilities.calculateCrownBaseHeight [Ddom, Hdom]) • Mäj les variables arbre moyen : <i>Hg</i> (Lub2Utilities.calculateHeight [Dg]), <i>CBHg</i> (Lub2Utilities.calculateCrownBaseHeight [Dg, Hg]), <i>Vg</i> (getVolume [Dg \times π \times Hg]) • Mäj les paramètres du modèle de croissance en diamètre : <i>DiameterGrowthThreshold</i> (Lub2Utilities.calculateDiameterGrowthThreshold), <i>S_sigma</i> (Lub2Utilities.calculateS_sigma) *** et <i>alpha</i> (Lub2Utilities.calculateAlpha) 	<p>GymnoStand.calcStand</p> <p>Après vérification que la hauteur des arbres est définie (sinon exception) :</p> <ul style="list-style-type: none"> • Mäj les caractéristiques moyennes du peuplement (<i>nTrees</i>, <i>nTreesHa</i>, <i>basalArea</i>, <i>cg</i>) en parcourant la liste des arbres (GymnoStand.calcMeanFeatures) • Mäj la hauteur dominante (<i>HDom</i>) à partir de la liste des arbres du peuplement*** : calcule la hauteur moyenne des arbres dominant du peuplement (GymnoStand.calcHDomFromTrees), les arbres dominants étant identifiés comme les <i>n</i> (= <i>Area</i> / 100) plus grands (si <i>n</i> est supérieur au nombre total d'arbre, alors <i>n</i> prend la valeur du nombre total d'arbre) • Mäj le <i>site index</i> au cas où une intervention ou une mortalité naturelle n'ai modifié le <i>Hdom</i> (GymnoStand.calcSiteIndex \rightarrow GymnoSpecies.calcSiteIndex \rightarrow GymnoSpecies.calcHDomFromBi [50 ans]) • Calcule et mäj l'incrément de circonférence des arbres dominants à partir du <i>site index</i> pour le modèle de Perin ***** (GymnoStand.calcDCircDom) • Mäj la circonférence dominante (<i>CDom</i>) à partir de la liste des arbres du peuplement (GymnoStand.calcCDom) (les arbres dominants sont identifiés comme dans GymnoStand.calcHdomFromTrees) • Calcule et mäj l'incrément en hauteur dominante de l'année suivante (<i>DHDom</i>) pour le modèle de croissance Deleuze ***** (GymnoStand.calcDHDom) • Calcule et mäj la <i>RDI</i> du peuplement (GymnoStand.calcRdi \rightarrow GymnoSpecies.calcRdi) • Mäj du volume sur pied du peuplement (GymnoStand.updateTreeVolume), calculé comme la somme du volume de tous les arbres (GymnoTree.tariff) 	<p>> Ignorer les seedlings dans le calcul des caractéristiques dynamiques et globalement dans le déroulement de l'ensemble des processus</p> <p>* S'il y a moins de 100 arbres par hectare, <i>Ddom</i> = <i>Dg</i>. La moyenne quadratique des diamètres (<i>Dg</i>) est donc calculée dans les variables des dominant et non dans les variables arbre moyen.</p> <p>** Conséquence sur la mäj de <i>HDom</i> :</p> <p>S'il y a plus de 100 arbres par hectare, le <i>Ddom</i> local est égale à <i>Ddom</i> calculé dans la méthode Lub2Utilities.calculateHeight, donc <i>HDom</i> ne change pas. Mais, s'il y a moins de 100 arbres par hectare, le <i>Ddom</i> local (= <i>Dg</i>) n'est pas égale à <i>Ddom</i> calculé dans la méthode Lub2Utilities.calculateHeight, donc <i>HDom</i> est mäj à la baisse.</p> <p>*** <i>S_sigma</i> correspond à la somme des circonférences des arbres strictement supérieures au seuil de diamètre de croissance (<i>GrowthThreshold</i>). <i>S_sigma</i> est utilisé dans le calcul de la pente <i>alpha</i>.</p> <p>**** Une autre méthode de calcul de la hauteur dominante (GymnoStand.calcHdomFromAge) est présente dans GymnoStand.calcInitialStand, qui est exécuté lors de la création d'un peuplement virtuel (GymnoModel.createVirtualStand) et lors du chargement d'un inventaire (GymnoModel.loadInitStand).</p> <p>***** Dans Gymnos, le modèle de Perin n'est plus utilisé, ne reste actif que le modèle Deleuze.</p>
	Mettre à jour le paramètre de croissance « seuil » (<i>diameterGrowthThreshold</i> vs <i>A</i>)	<p>Lub2Utilities.calculateDiameterGrowthThreshold, calcule le seuil de circonférence par itérations</p> <p>Soit l'intervalle de Dbh borné par <i>diameterBegin</i> (= 0 à l'initiation) et <i>diameterEnd</i> (= Dbh du plus gros arbre à l'initiation) :</p> <ul style="list-style-type: none"> • Tant que l'intervalle (<i>diameterEnd</i> – <i>diameterBegin</i>) est plus grand que $0.001 \times diameterEnd$: <ul style="list-style-type: none"> - Calcule le diamètre médian de l'intervalle (<i>diameterMiddle</i>) - Calcule la somme des Dbh au-dessus de <i>diameterMiddle</i> (<i>S_sigma</i>) - Calcule le nombre d'arbre au-dessus de <i>diameterMiddle</i> (<i>N_</i>) - Calcule du seuil (<i>threshold_</i>) en fonction de <i>N_</i>, <i>S_sigma</i> et de deux constantes (<i>mu</i> et <i>lambda</i>) - Si le seuil calculé (<i>threshold_</i>) est inférieure au diamètre médiant de l'intervalle (<i>diameterMiddle</i>), l'intervalle est réduit de moitié par le haut (<i>diameterEnd</i> = <i>diameterMiddle</i>) - Sinon, l'intervalle est réduit de moitié par le bas (<i>diameterBegin</i> = <i>diameterMiddle</i>) 	Inclus dans GymnoTree.processGrowth	<p>* <i>S_sigma</i> est utilisé dans le calcul du seuil de circonférence (<i>GrowthThreshold</i>). <i>S_sigma</i> correspond à la somme des circonférences des arbres strictement supérieures au seuil de circonférence (<i>GrowthThreshold</i>). Puisqu'il se fait référence à lui-même, il est nécessaire de calculer <i>GrowthThreshold</i> par itération.</p>
	Mettre à jour le paramètre de croissance « pente » (<i>alpha</i> vs <i>P</i>)	<p>Lub2Utilities.calculateAlpha</p> <ul style="list-style-type: none"> • Calcule l'accroissement en hauteur dominante (<i>annualGrowthInHdom</i>) en fonction de l'âge de l'unité de croissance (Lub2Utilities.calculateAnnualGrowthInHdom) • Calcule <i>alpha</i> : $alpha = [8037 + 287.09 \times 100 \times annualGrowthInHdom] \times 4.29714e-5 \times Math.exp(-9.52169e-6 \times s_sigma)$ • Retourne <i>alpha</i> 	Inclus dans GymnoTree.processGrowth	

Processus général	Méthode / Étape	Luberon2	Gymnos	Point de développement (>) et remarque (*)
Mortalité par auto-éclaircie	Exécuter la mortalité par auto-éclaircie	<p>Lub2Model.process[...Mortality¹</p> <ul style="list-style-type: none"> • Ajoute les arbres dans la liste <i>sortedTrees</i> où ils sont triés par ordre croissant de <i>Dbh</i> (capsis.util.TreeDbhComparator) • Calcule la densité d'arbres par hectare (<i>treeDensity</i>) et la moyenne quadratique des circonférences (<i>Cg</i>) • Tant que <i>treeDensity</i> dépasse le seuil d'auto-éclaircie (fonction de <i>Cg</i>), supprime les arbres de la scène dans l'ordre de <i>sortedTrees</i> (càd du plus petit <i>Dbh</i> au plus grand) : <p>- Retire l'arbre de la scène (newScene.removeTree / tree.setNumber¹)</p> <p>- Si l'arbre s'est déjà reproduit, il est ajouté à la liste <i>deadTreeList</i></p> <p>- Màj <i>treeDensity</i> et <i>Cg</i></p> <p>- Si la boucle est répétée plus d'un million de fois ou qu'il n'y a plus d'arbres ou que la moyenne quadratique des circonférences est nulle : arrête la boucle</p>	<p>GymnoModel.runMortality</p> <ul style="list-style-type: none"> • Calcule la densité relative du peuplement (<i>rdiStand</i>) à partir de la nouvelle scène et la densité relative maximum (<i>rdiMax</i>) à partir de la scène de référence et de la nouvelle scène • Calcule le <i>Dbh</i> maximum (<i>maxDbh</i>) et le <i>Dbh</i> minimum (<i>minDbh</i>) de la scène depuis la collection <i>trees</i> • Crée la liste <i>arrayTree</i> pour y ajouter chaque arbre de la scène, avec un score de sélection pour élimination en parti stochastique^{**} : <p>- Si <i>maxDbh</i> égale <i>minDbh</i> (càd si tous les arbres sont identiques en <i>Dbh</i> ou s'il n'y a qu'un seul arbre dans la scène), ajoute tous les arbres (<i>ScoredTree</i>) avec un score de 1</p> <p>- Sinon, ajoute tous les arbres (<i>ScoredTree</i>) avec un score égal à : $[(treeDbh - minDbh) / (maxDbh - minDbh)] \times random(0.0; 1.0)$</p> <ul style="list-style-type: none"> • Trie les arbres de la liste <i>arrayTree</i> par ordre croissant de <i>score</i> • Tant que <i>rdiStand</i> est supérieur à <i>rdiMax</i>, supprime de la scène les arbres dans l'ordre de la liste <i>arrayTree</i> (càd du plus bas <i>score</i> vers le plus haut) : <p>- Soit un boolean <i>doMortality</i> = True ; tant que <i>doMortality</i> est vrai :</p> <p>- Si le nombre d'arbre de la scène est inférieur ou égale à 1, arrête la mortalité (<i>doMortality</i> = False), sinon la mortalité a lieu dans l'ordre de la liste <i>arrayTree</i> :</p> <ul style="list-style-type: none"> o Recalcule la densité relative du peuplement (<i>rdiStand</i>) en décomptant l'arbre considéré o Si <i>rdiStand</i> supérieur à <i>rdiMax</i>, retire l'arbre de la scène o Sinon (si <i>rdiStand</i> <= <i>rdiMax</i>), arrête la mortalité (<i>doMortality</i> = False) 	<p>* S'il s'agit d'un arbre unique (effectif = 1), il est supprimé de la scène à l'aide de la méthode newScene.removeTree, mais s'il s'agit d'un arbre multiple (effectif > 1), son effectif est recalculé à la baisse (-1 ou -1% si l'effectif supérieur à 100) et est affecté via la méthode tree.setNumber.</p> <p>** Dans Gymnos, la mortalité par auto-éclaircie est partiellement stochastique.</p>
Impacts de perturbations	Exécuter les impacts de type mortalité	<p>Lub2Disturbances.execute</p> <ul style="list-style-type: none"> • Calcule l'intensité annuelle de la perturbation (<i>disturbanceIntensity</i>, mesurée en termes de probabilité maximum de mortalité) (Lub2Disturbances.calculateDisturbanceIntensity) de toute la scène à partir de lois de distributions Weibull (Lub2Disturbances.generateWeibullLaw) dont les paramètres sont spécifiés dans l'inventaire • Pour chaque pixel de chaque <i>MainParcel</i> : <p>- Calcule la somme des hauteurs de houppiers (<i>crownHeightSum</i>) en parcourant la liste des arbres</p> <p>- Calcule la probabilité de mortalité dans le pixel : <i>globalProba</i> = $(disturbanceIntensity \times crownHeightSum) / (1.0 + crownHeightSum)$</p> <p>- Pour chaque arbre du pixel : calcule la probabilité de mortalité individuelle (<i>individualMortalityProbability</i>) comme la somme entre <i>globalProba</i> et un effet génétique individuel de sensibilité (<i>GeneticTree.getGeneticValue("disturbanceSensibility")</i>^{*)} ; tire un nombre aléatoire entre 0.0 et 1.0 (<i>randomValue</i>) ; supprime l'arbre de la scène si <i>randomValue</i> est inférieure ou égale à <i>individualMortalityProbability</i></p>	<p>GymnoModele.runNewBarkPeeling^{**}</p> <p>GymnoModele.updateOldBarkPeelingDamage^{**}</p>	<p>* L'effet génétique individuel est décrit dans la case rose « Valeurs individuel génétiques / phénotypiques ».</p> <p>** Non développé car ne sera pas importé dans Luberon2</p>

Processus général	Méthode / Étape	Luberon2	Gymnos	Point de développement (>) et remarque (*)
	<i>Impacter la croissance des arbres individuels en fonction de leur sensibilité et du niveau de stress hydrique</i>			> Impacter la croissance d'un arbre moyen de <i>DBH</i> donné en fonction du niveau de stress de l'unité de croissance, de la sensibilité moyenne du peuplement et d'un effet individuel (cf. partie Valeurs individuel génétiques / phénotypiques) > Induire de la mortalité par faible croissance avec un effet de seuil (Bugmann, 1996)
	<i>Simuler des régimes de stress hydrique stochastiques</i>			> Implémenter une distribution de probabilité du stress modulée par le <i>LAI</i> > Ajouter une représentation graphique du régime de stress hydrique moyen de la scène
	<i>Modéliser la surface foliaire spécifique pour moduler le niveau de stress hydrique</i>			> Simuler la valeur de <i>LAI</i> des unités de croissance avec le modèle de Nicholas J. Smith (1993) du sapin douglas > Ajouter une inertie temporelle au <i>LA</i> des arbres individuels pour simuler la persistance de l'effet de l'auto-éclaircie sur le couvert (Non abouti)
Régénération	<i>Exécuter la régénération sous conditions au niveau du pixel</i>	Lub2Model.runRegeneration <ul style="list-style-type: none"> Identifie les arbres fertiles de la scène (<i>DBH</i> supérieur ou égale au <i>DIAMETER_FERTILITY</i>) et calcule leur fécondité en nombre de graines produites en fonction de leur <i>DBH</i> et de façon stochastique (modèle de François Courbet) dans les listes <i>fertileTreeList</i> et <i>fecundityList</i>, attribués de la scène (<code>Lub2Model.identifyFertileTrees</code>) Pour chaque pixel de chaque placette, si le nombre d'arbre adulte est inférieur ou égale à 3 et si le nombre d'année écoulé depuis la première régénération est inférieur ou égale à 3 : <ul style="list-style-type: none"> Exécution de la régénération (<code>Lub2Regeneration.execute</code>) Définit l'âge de première régénération s'il n'est pas défini. Màj des variables peuplement du pixel (<code>Lub2Utilities.calculateDynamicCharacteristics</code>) 		> Permettre à plus de deux générations de se succéder > Les processus de régénération sont totalement absents de Gymnos : adapter les processus de régénération de Luberon2 au sapin Douglas (partiellement abouti) > Optimiser la méthode <code>getTree</code> et le bouclage sur les <i>seedlings</i> pour accélérer le modèle
	<i>Générer les nouveaux plants à la taille de l'âge de recrutement</i>	Lub2Regeneration.execute <ul style="list-style-type: none"> Génère des nouveaux semis, en particulier leur génotype par identification de la mère et du père (<code>Lub2Regeneration.regenerationStep</code>) Génère un tableau de probabilités des <i>Dbh</i> à l'âge de recrutement (<code>Lub2Utilities.generateWeibullLaw</code>) et tire des valeurs aléatoires de <i>Dbh</i> pour les attribuer aléatoirement aux semis 		> attribuer un <i>DBH</i> initial aux semis de sapin Douglas : adapter la méthode <code>GymnoModel.createVirtualStand</code> * <code>Lub2Utilities.generateWeibullLaw</code> est aussi appelée par <code>Lub2Model.initializeModel</code> au moment de la création du projet si le <i>Dbh</i> est non spécifié dans l'inventaire.

Processus général	Méthode / Étape	Luberon2	Gymnos	Point de développement (>) et remarque (*)
	Générer les nouveaux semis	<p>Lub2Regeneration.regenerationStep Pour chaque arbre fertile de la scène (liste <i>fertileTrees</i>) :</p> <ul style="list-style-type: none"> • Si l'option voisinage (NEIGHBORHOOD) est choisie, identifie les arbres voisins (Lub2RoundMask) et ajoute les fertiles à la liste <i>fertilNeighbourTrees</i> pour plus tard déterminer les pères • Détermine le flux de graines de la mère vers le pixel (<i>flow</i>) (Lub2Spread.seedlingsFlow) en fonction de la fécondité de la mère (getFecondity) et de la distance <i>dist</i> entre le pixel et la mère (Lub2Regeneration.dist) • Crée les nouveaux semis en nombre égale au flux de graine (flow) : <ul style="list-style-type: none"> - Tire une position <i>x</i> et <i>y</i> aléatoire au futur semi et vérifie ; vérifie si le point est dans le pixel, sinon retire <i>x</i> et <i>y</i> - Trouve le père (Lub2Regeneration.wholsTheFather) * : si l'option voisinage est activée, effectue le tirage d'un père dans la liste <i>fertilNeighbourTrees</i>, sinon dans la liste <i>fertileTrees</i>. - Crée le semi (new Lub2GeneticTree) et l'ajout à la scène (scene.addTree) - Attribue un génotype au semi sachant l'identifiant du père et de la mère (newTree.getGenotype)** 		<p>* Lors de la sélection du père, la gestion du cas où aucun père n'est trouvé (<i>fatherId</i> == -1) est en commentaire. Comment est gérée cette exception ? Dans la super classe GeneticTree ?</p> <p>** La méthode <i>getGenotype</i> est décrite dans la case rose « Valeurs individuel génétiques / phénotypiques ».</p>
	Déterminer le père des semis en fonction des choix utilisateur	<p>Lub2Regeneration.wholsTheFather</p> <ul style="list-style-type: none"> • Si la liste des pères potentiels est vide, renvoie -1 • Calcule le vecteur des contributions polliniques cumulées des pères potentiels (<i>contribs</i>), associé au vecteur des identifiants des pères potentiels (<i>fatherListId</i>) en parcourant la liste des pères potentiels : <p>- Lorsque le père potentiel correspond à la mère : si SELFING autorisé, calcule de la <i>contribSelf</i> (= <i>Dbh</i>²) et de <i>idSelf</i> pour les ajouter plus tard aux vecteurs <i>contribs</i> et <i>fatherListId</i>, sinon passe au père potentiel suivant</p> <p>- Si option PANMIXIA, calcule la contribution pollinique cumulée (<i>pollenFlowCum</i>) tels que chaque père a une contribution individuelle égale à 1, puis l'ajoute au vecteur <i>contribs</i> (<i>contribs</i> ressemble donc à 1, 2, 3, 4, [...]) ; ajoute l'identifiant de chaque père au vecteur <i>fatherListId</i></p> <p>- Sinon, calcule de la fécondité mâle (<i>malefecundity</i>) comme le carré du <i>Dbh</i> et attribue la valeur 1 à la densité de probabilité du pollen (<i>densProbPollen</i>) (correspond à l'option NEIGHBORHOOD)</p> <p>Mais, si option POLLEN_DISPERSION_KERNEL, recalcule de la densité de probabilité du pollen <i>densProbPollen</i> (Lub2Spread.densProbPollen) en fonction de la distance entre la mère et le père potentiel (Lub2Regeneration.distanceFromTreeToTree)</p> <p>Calcule la contribution pollinique cumulée (<i>pollenFlowCum</i>) tels que chaque père a une contribution individuelle égale à <i>malefecundity</i> × <i>densProbPollen</i>, puis l'ajoute au vecteur <i>contribs</i> ; ajoute l'identifiant de chaque père au vecteur <i>fatherListId</i></p> <ul style="list-style-type: none"> • Traite le cas du selfing : si <i>contribSelf</i> est non nul, ajoute <i>contribSelf</i> et de <i>idSelf</i> dans les vecteurs <i>contribs</i> et <i>fatherListId</i> • Tire aléatoirement un père dans le vecteur <i>fatherListId</i> : <p>- Calcule un nombre aléatoire (<i>randomValue</i>) en multipliant la contribution pollinique cumulée (<i>pollenFlowCum</i>) par un nombre aléatoire entre 0.0 et 1.0</p> <p>- Sélectionne dans le vecteur <i>fatherListId</i>, l'identifiant du père correspondant à la première valeur du vecteur <i>contribs</i> à être supérieur à <i>randomValue</i></p> <ul style="list-style-type: none"> • Renvoie l'identifiant du père sélectionné 		

Processus général	Méthode / Étape	Luberon2	Gymnos	Point de développement (>) et remarque (*)
Masting	Simuler une dynamique de masting			> Ajouter une pulsation de production de graine toutes les x années, plus un effet stochastique (Non abouti)
Valeurs génétiques / phénotypiques individuelles (Cf. documentation de la bibliothèque génétique Capsis)	Simuler le génotype d'un (nouvel) arbre connaissant ses parents	GeneticTree.getGenotype Simule et affecte le génotype (<i>IndividualGenotype</i> / <i>MultiGenotype</i> ³) d'un arbre : • Identifie le père et la mère de l'arbre considéré à partir de leurs identifiants respectifs (<i>GeneticTree.searchTree</i>) • Simule le processus de la méiose (<i>Genotype.getGamete</i>) • Simule la fusion des gamètes (<i>Genotype.fuseGametes</i>)		
	Calculer la valeur phénotypique d'un individu pour le caractère « vigueur »	GeneticTree.getPhenoValue("diameterGrowth_cm") → <i>AlleleEffect.getPhenoValue</i> Calcule, pour un arbre donné, sa valeur phénotypique « vigueur » comme la somme de sa valeur génétique (<i>GeneticTree.getGeneticValue</i>), sa valeur environnementale fixe (<i>GeneticTree.getFixedEnvironmentalValue</i>) et sa valeur inter environnementale de l'étape en cours**.		> Effet individuel « vigueur » à passer sur l'accroissement en diamètre * <i>getFixedEnvironmentalValue</i> tire aléatoirement la valeur environnementale fixe dans une loi normale de moyenne 0 et de variance la variance environnementale intra étape (la variance environnementale total multipliée par 1 - la part de variance environnementale inter étape donnée dans l'inventaire ; la variance environnementale total pouvant être donnée dans l'inventaire ou être déduite de l'héritabilité). Si la valeur a déjà été calculée, elle est conservée au niveau de l'arbre ; l'appel sur un <i>GeneticTree</i> ne fait alors que renvoyer cette valeur. ** La valeur inter environnementale est tirée lors de chaque étape dans une loi normale de moyenne 0 et de variance la variance inter environnementale (la variance environnementale total multipliée par la part de variance environnementale inter étape donnée dans l'inventaire).
	Calculer la valeur génétique d'un individu pour le caractère « sensibilité sécheresse en termes de mortalité »	GeneticTree.getGeneticValue("disturbanceSensibility") → <i>AlleleEffect.getGeneticValue</i> (si premier appel) Calcule, pour un arbre donné, sa valeur génétique « sensibilité sécheresse en termes de mortalité » sous l'hypothèse d'additivité des valeurs alléliques, à partir de son génotype (<i>IndividualGenotype</i> / <i>MultiGenotype</i> ³), du <i>AlleleDiversity</i> de l'espèce et du <i>ParameterEffect</i> du caractère/paramètre (si la valeur a déjà été calculée, elle est conservée au niveau de l'arbre ; l'appel sur un <i>GeneticTree</i> ne fait alors que renvoyer cette valeur)		> Le choix avait été fait d'utiliser comme valeur individuelle la valeur génétique plutôt que la valeur phénotypique, car la somme des hauteurs des houppiers, qui module l'intensité de perturbation, représente déjà une part environnementale. Peu pertinent : utiliser la valeur phénotypique
	Calculer la valeur individuelle (génétique / phénotypique) pour le caractère « sensibilité sécheresse en termes de croissance »			> Ajouter un effet individuel phénotypique pour la sensibilité de la croissance à la sécheresse

¹ Les crochets [...] remplacent « Pixel » et « LateralParcel » : dans Luberon2, deux types de méthodes coexistent, l'une est adaptée aux *MainParcel*, qui sont constituée de plusieurs unités de croissances indépendantes nommées pixel, l'autre est adaptée aux *LateralParcel* représentant chacune une unité de croissance. Dans mes simulations, uniquement des *MainParcel* ont été utilisées.

² Les méthodes soulignées sont décrites à la suite dans une case « Méthode / Étape » avec plus de précision.

³ Il existe deux types de génotypes : pour les arbres individualisés des *mainParcel* portant un génotype individuel et fixe, et pour les arbres multiples des *lateralParcel* portant un génotype multiple. Dans mes simulations, uniquement des *MainParcel* et des arbres individualisés ont été utilisés.

Récapitulatif des principaux paramètres pouvant varier d'une espèce à l'autre dans Luberon2

Dans le cadre de mes travaux, les valeurs pour le sapin Douglas sont tirées de Perin et al. (2013, 2017) pour les paramètres de croissance, de OCDE (2010) pour les paramètres de reproduction et de régénération différents du cèdre, de Fririon et al. (2023) pour les valeurs génétiques, de la réanalyse des données de Petit-Cailleux (2021) pour les paramètres de perturbation diffuses, de Bugmann (1996) pour les paramètres de mortalité par faible croissance et de l'analyse des données pédo-climatiques de l'aire de répartition européenne du sapin Douglas pour les paramètres de perturbation sécheresse (Article 4). Le tableau ci-dessous indique où l'information est donnée dans le modèle : dans la fiche espèce, dans l'inventaire ou calculée dans le code. Le tableau ne donne pas une liste exhaustive des processus démographiques (HDom, self-thinning, etc.) devant être formalisés pour chaque espèces mais la liste des paramètres et variables communs.

Paramètre commun	Douglas	Cèdre
Processus démographiques (croissance, reproduction et régénération)		
<i>modèle de croissance : seuil de circonférence (A / diameterGrowthGirthThreshold)</i>	calculé dans Lub2DouglasUtilities	calculé dans Lub2CedrusUtilities
<i>modèle de croissance : pente (P / diameterGrowthAlpha)</i>	calculé dans Lub2DouglasUtilities	calculé dans Lub2CedrusUtilities
<i>modèle de croissance : flexibilité (m / diameterGrowthThresholdFlexibility)</i>	calculé dans Lub2DouglasUtilities	fixé à 1 dans Lub2CedrusUtilities
<i>gamme de Site index (HDom à 50 ans)</i>	inventaire (ex. 28 - 32 - 40 - 44 ; 36 en moyenne)	inventaire (ex. 11 - 15 - 18 - 21)
<i>diamètre minimal de fécondité (diameterFertility)</i>	fiche espèce (10)	fiche espèce (15)
<i>Fécondité mâle (contribution pollinique) et femelle (nombre de fruits)</i>	calculés dans Lub2DouglasRegeneration	calculés dans Lub2CedrusRegeneration
<i>nombre de graines viables par fruit (seedNumberPerFruit)</i>	fiche espèce (8)	fiche espèce (80)
<i>âge de recrutement des semis par le modèle (recruitmentAge)</i>	fiche espèce (15)	fiche espèce (25)
<i>durée max de cumul des semis (seedlingDuration)</i>	fiche espèce (3)	fiche espèce (3)
<i>nb max d'adultes dans un pixel pour accueil de semis (maxNumberOfAdultTrees)</i>	fiche espèce (3)	fiche espèce (3)
<i>distance max de dispersion du pollen (maxPollinationDistance)</i>	fiche espèce (150)	fiche espèce (150)
<i>paramètre delta de dispersion graines (deltaSeed)</i>	fiche espèce (240)	fiche espèce (240)
<i>paramètre b dispersion graines (bSeed)</i>	fiche espèce (0.22)	fiche espèce (0.22)
<i>paramètre delta dispersion pollen (deltaPollen)</i>	fiche espèce (100)	fiche espèce (100)
<i>paramètre b dispersion pollen (bPollen)</i>	fiche espèce (0.3)	fiche espèce (0.3)
<i>taux d'autofécondation (selfingRate)</i>	fiche espèce (0.05)	fiche espèce (0.05)
Variabilité génétique		

<i>sensibilité moyenne de la population au stress (growthDisturbanceMeanPlasticity)</i>	inventaire (ex. 0.002)	inventaire (ex. 0.002)
<i>vigueur moyenne de la population (growthMeanValue)</i>	inventaire (ex. 0)	inventaire (ex. 0)
<i>VA vigueur (expectedAdditiveVariance, growthVigor_cm)</i>	inventaire (ex. 0.00348)	inventaire (ex. 0.00348)
<i>VA sensibilité au stress (expectedAdditiveVariance, growthDisturbanceIndividualSusceptibility)</i>	inventaire (ex. 0.0000006)	inventaire (ex. 0.0000006)
<i>VA sensibilité à la mortalité diffuse (expectedAdditiveVariance, mortalityDisturbanceIndividualSusceptibility)</i>	inventaire (ex. 0)	inventaire (ex. 0)
<i>h² vigueur (heritability, growthVigor_cm)</i>	inventaire (ex. 0.3)	inventaire (ex. 0.3)
<i>h² sensibilité au stress (heritability, growthDisturbanceIndividualSusceptibility)</i>	inventaire (ex. 0.3)	inventaire (ex. 0.3)
<i>h² sensibilité à la mortalité (heritability, mortalityDisturbanceIndividualSusceptibility)</i>	inventaire (ex. 0)	inventaire (ex. 0)
<i>Valeur de la dépression de consanguinité pour F=1 (inbreedingDepression)</i>	fiche espèce (ex. 0.12 [non abouti])	fiche espèce (ex. 0.12 [non abouti])
Régimes de perturbation		
<i>mortalité diffuse : paramètre alpha faible intensité (mortalityDisturbance_alphaWeak)</i>	inventaire (ex. 2.9447201)	inventaire (ex. 2.9447201)
<i>mortalité diffuse : paramètre beta faible intensité (mortalityDisturbance_betaWeak)</i>	inventaire (ex. 0.0221433)	inventaire (ex. 0.0221433)
<i>mortalité diffuse : paramètre alpha forte intensité (mortalityDisturbance_alphaStrong)</i>	inventaire (ex. 0)	inventaire (ex. 0)
<i>mortalité diffuse : paramètre beta forte intensité (mortalityDisturbance_betaStrong)</i>	inventaire (ex. 0)	inventaire (ex. 0)
<i>mortalité faible croissance : seuil d'accroissement faible en diamètre (weakGrowthThreshold_cm)</i>	fiche espèce (0.03)	fiche espèce (0.03)
<i>mortalité faible croissance : seuil d'accroissement faible en taux de croissance (weakGrowthThreshold_Rate)</i>	fiche espèce (0.1)	fiche espèce (0.1)
<i>mortalité faible croissance : probabilité de mortalité associée à un accroissement faible (weakGrowthMortalityProbability)</i>	fiche espèce (0.368)	fiche espèce (0.368)
<i>stress level : paramètre a de la relation GammaShape ~ LAI</i>	inventaire (ex. 55.90)	inventaire (ex. 55.90)
<i>stress level : paramètre b de la relation GammaShape ~ LAI</i>	inventaire (ex. -5)	inventaire (ex. -5)
<i>stress level : paramètre c de la relation GammaShape ~ LAI</i>	inventaire (ex. 7.41)	inventaire (ex. 7.41)
<i>stress level : paramètre a de la relation GammaScale ~ LAI</i>	inventaire (ex. -12.06)	inventaire (ex. -12.06)
<i>stress level : paramètre b de la relation GammaScale ~ LAI</i>	inventaire (ex. -1)	inventaire (ex. -1)
<i>stress level : paramètre b de la relation GammaScale ~ LAI</i>	inventaire (ex.9.45)	inventaire (ex.9.45)

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