Biodiversité
Gestion Forestière
& Politiques Publiques

PROGRAMME DE RECHERCHE

"BIODIVERSITE, GESTION FORESTIERE ET POLITIQUES PUBLIQUES"

TITRE DU PROJET EN FRANÇAIS
« Potentiel de régénération des chênaies
dans le contexte du changement climatique:
Quel avenir pour le masting et les consommateurs de glands ? »

Acronyme : « PotenChêne »

TITRE DU PROJET EN ANGLAIS
"Oak forest regeneration in the perspective of climate change:
What's next for masting and oak acorn consumers?"

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Rapport Scientifique
du programme « Potenchêne »

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RAPPEL DE LA PROPOSITION INITIALE

Le programme ‘Potenchêne’ vise à apporter un éclairage nouveau sur les capacités des chênaies à faire face au changement climatique en se focalisant sur la phase de régénération. Nous nous focalisons sur le devenir du *masting* du chêne (patron de reproduction caractérisé par des fructifications massives, intermittentes et synchronisées à l’échelle d’une population d’arbres) et sur le devenir des consommateurs de glands qui sont susceptibles de fortement impacter la démographie des chênes. Nous nous focalisons sur trois espèces d’ongulés d’intérêt cynégétique (sanglier, cerf, chevreuil) et sur des communautés composées de 4 espèces d’insectes parasites des glands. Ce projet s’articule selon quatre axes. L’axe 1 vise à mieux comprendre les mécanismes proximaux qui sous-tendent le masting du chêne en intégrant les processus endogènes à l’arbre (allocation de ressources dans la floraison (pollen, fleurs femelles), la fructification, et la croissance végétative) et les conditions environnementales (disponibilité en pollen environnant l’arbre, conditions météorologiques). L’axe 2 explore la dynamique « glandée-consommateurs de glands-régénération des chênaies ». Dans ce projet, nous nous focaliserons sur trois espèces d’ongulés d’intérêt cynégétique (sanglier, cerf, chevreuil) et sur des communautés composées de 4 espèces d’insectes parasites des glands. L’axe 3 vise à explorer différents scénarios sur le devenir du masting du chêne et de la dynamique « glandée-consommateurs de glands-régénération des chênaies» dans le contexte du changement climatique. L’axe 4 est dédié au développement d’outils et méthodes à l’intention des gestionnaires. En particulier, nous visons à quantifier et anticiper, dès le printemps, les glandées automnales, contribuant ainsi à optimiser la procédure de régénération des chênaies et le contrôle des populations d’ongulés.

Les méthodes utilisées ainsi que les références bibliographiques sont détaillées dans les articles présentés dans les annexes du rapport scientifique. Ce rapport fait référence à des éléments confidentiels (encore non publiés) qui sont détaillés dans le fichier correspondant à la « Partie Confidentielle » du rapport scientifique (les références à ces parties sont codifiées comme suit : RS.Part_Conf_numero).

PARTIE 1: CAUSES PROXIMALES DU MASTING

Partie 1.1: Impact des températures printanières sur l'intensité des glandées (BioGeCo, ONF, LBBE) (Caignard *et al.* 2017, Annexe A1)

La fitness ou valeur adaptative caractérise la capacité d'un arbre à survivre et transmettre ses gènes à la génération suivante. Le succès de reproduction, l'une des composantes majeures de la fitness, a jusqu'ici été très peu étudié chez les chênes en milieu forestier. Aucune étude à long terme de l'effort de fructification sur une large échelle spatiale n'a notamment été réalisée à ce jour (avec plusieurs populations sur un vaste territoire) afin de pouvoir prédire l'évolution de la reproduction sous l'effet du changement climatique. Grâce à un jeu de données unique mis à disposition par l'ONF dans le cadre du programme 'Potenchêne', et un suivi intensif de la reproduction le long d'un gradient altitudinal, le laboratoire BioGeCo a pu caractériser la réponse de l'effort de reproduction à la température. La reproduction de 28 populations de chênes (sessiles et pédonculés), réparties sur l'ensemble de la France métropolitaine, a été suivie de 1994 à 2007. Au cours des deux dernières décennies, nous avons observé une augmentation marquée de la production fruitière moyenne pour ces deux espèces. Cette accentuation de l'effort de reproduction des chênes est positivement corrélée à l'augmentation des températures printanières observée au cours des deux dernières décennies (Fig. 1). La force de notre étude était donc de pouvoir estimer la sensibilité de la production fruitière au cours du temps sur plusieurs populations indépendantes les unes des autres et réparties sur une large échelle géographique. L'effet positif de la température sur le niveau moyen de reproduction du chêne a été confirmé grâce au gradient altitudinal.

On retrouve très peu de patrons temporels de la production de graines dans la littérature, dû à la difficulté d'effectuer des suivis *in situ*. Chez *Pinus engelmannii* et *Nothofagus solandri* des patrons similaires (augmentation avec la température) ont toutefois été observés. Mais à ce jour, une grande partie des travaux sur la reproduction des arbres a porté sur des espèces de milieux méditerranéens, et notamment sur les chênes américains et les chênes du sud de l'Europe. Ces derniers montrent, contrairement à nos résultats, que la reproduction des chênes méditerranéens est affectée négativement par un réchauffement du climat, en réponse à la diminution de la disponibilité en eau. Nos résultats suggèrent que la température a et pourrait avoir un effet positif sur la production de graines tant que la disponibilité en eau n'est pas limitante en zone tempérée.

Ces patrons suggèrent une augmentation de l'intensité des glandées chez les chênes tempérés européens, favorable au maintien des populations de chêne dans leurs environnements. Cependant, de manière comparable à la croissance, la reproduction des chênes tempérés semble être favorisée par le réchauffement à condition que la disponibilité en eau ne soit pas limitante. Par ailleurs, il est actuellement difficile d’estimer et de prédire l’impact du changement climatique sur la fluctuation temporelle de ces épisodes de glandées (masting des chênes). Des fructifications plus importantes mais plus régulières d’une année sur l’autre pourraient diminuer l’avantage évolutif du masting.

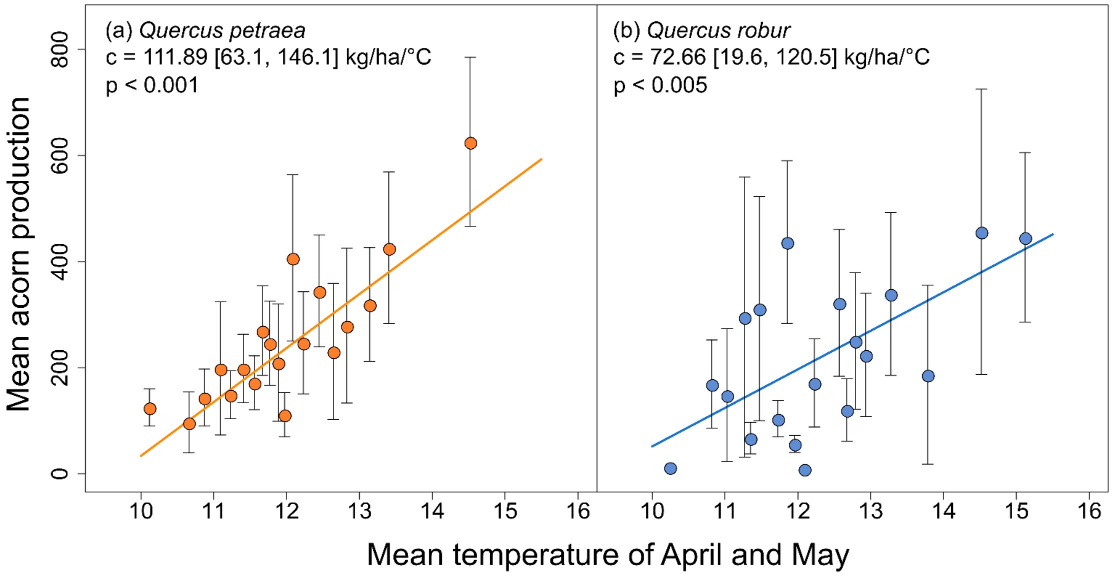

Figure 1. Impact des températures printanières sur l’intensité des glandées chez le chêne sessile (*Quercus petraea*) et le chêne pédonculé (*Q. robur*)

Partie 1.2: les modèles mécanistes du masting revisités (LBBE, BioGeCo, ONF ; Venner *et al.* 2016, Annexe A2)

Un ensemble de travaux traitant des mécanismes du masting formulent l'hypothèse que les plantes pérennes fructifient de façon synchronisée parce qu'elles rencontrent des conditions météorologiques similaires et y répondent de la même manière à travers leur allocation dans la reproduction. En parallèle, des études théoriques fondées sur les modèles d'acquisition et d'allocation de ressources (Resource budget model: RBM) ont proposé que le masting résulte de deux processus interactifs n'exigeant pas de fluctuations météorologiques: (i) la dynamique des ressources internes des arbres conduisant à un épuisement de celles-ci suite à un épisode de forte fructification et (ii) le processus de pollinisation croisée (les fleurs femelles d'un arbre ne peuvent pas être pollinisées par le pollen du même arbre), le succès de pollinisation étant considéré comme dépendant de la densité en pollen produit par les autres arbres (limitation pollinique). Ce processus pourrait conduire à la synchronisation des dynamiques des fructifications entre les arbres: tout arbre se reproduisant de manière asynchrone, en allouant massivement dans la floraison alors que les autres arbres produisent peu de fleurs (et donc peu de pollen), devrait connaître un très faible succès de pollinisation (lié à la faible densité en pollen exogène) et de fructification ; la ressource économisée en l'absence de fructification pourrait alors être à nouveau allouée dans la floraison l'année suivante, potentiellement en synchronie avec les autres arbres de la population. De fortes variations interannuelles de la fructification seraient ainsi favorisées par l'alternance d'années de forte et faible disponibilité en pollen produit de manière synchronisée par les arbres de la population.

Nous avons revisité les RBMs, d'une part, pour examiner l'impact du processus de pollinisation (et plus précisément de la sensibilité de la pollinisation à la disponibilité en pollen) sur le masting, et d'autre part, pour lier explicitement le masting à d''autres caractères reproducteurs des arbres (allocation de ressource dans la floraison et la fructification). Alors que la pollinisation croisée est le mécanisme clé qui synchronise la fructification dans les RBMs, notre modèle a montré que le masting est d'autant plus intense (Coefficient de variation temporelle, à l'échelle de la population – CVp) que la pollinisation est peu efficace (Fig. 2A et 2D, cercle vide). Lorsque la pollinisation est très efficace (cercle plein), un masting modéré peut néanmoins se produire à condition que les coûts de la floraison femelle (par rapport à la production de pollen) et de la fructification soient très élevés (coefficient de déplétion DC élevé –axe des abscisses-). Notre travail met en évidence le cadre puissant des RBMs – intégrant des paramètres biologiques explicites - pour lier la dynamique de fructification à divers traits reproducteurs et, finalement, fournir de nouvelles perspectives sur les stratégies de reproduction des plantes pérennes.

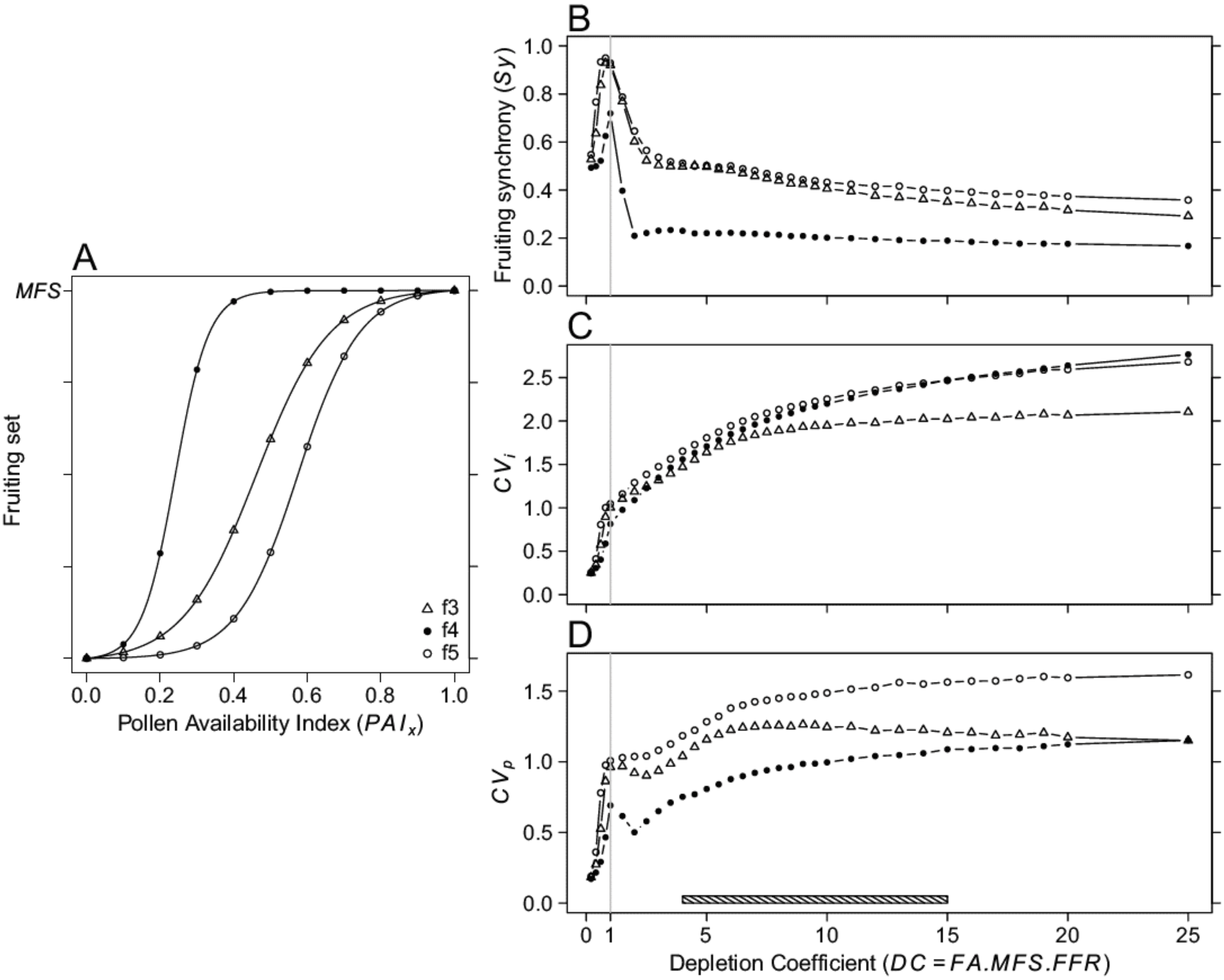

Figure 2. Impact de l'efficacité de la fonction de pollinisation sur la dynamique de fructification. Trois fonctions logistiques de pollinisation ont été testées :

$f_3: P_x(t) = \frac{1}{1+100.e^{-10.PAI_x(t)}}$; $f_4: P_x(t) = \frac{1}{1+200.e^{-22.PAI_x(t)}}$;$f_5: P_x(t) = \frac{1}{1+1000.e^{-12.PAI_x(t)}}$.

Pour chaque fonction de pollinisation, nous évaluons l’impact du coefficient d’épuisement des réserves (« DC », axe *X*) sur la synchronie de fructification entre les arbres « Sy » (B), sur l’intensité des fluctuations des fructifications à l’échelle des individus arbres « CVi » (C) ou à celle de la population « CVp » (D). La barre horizontale hachurée au-dessus de l'axe des abscisses indique la gamme de DC estimée empiriquement pour les chênes sessiles.

Partie 1.3 : Le pollen au cœur du masting (Schermer *et al.* soumis, RS.Part_Conf 1.1, 1.2, 1.3).

Nous montrons que le processus de pollinisation constitue la pierre angulaire du masting en étant impliqué dans deux processus **(RS.Part_Conf 1.1)**: (i) la dynamique des émissions polliniques locales suit un rythme biennal en accord avec l'hypothèse selon laquelle la production de pollen d'un arbre est régulièrement limitée par les ressources; (ii) la diffusion pollinique s'avère très sensible aux conditions météorologiques printanières qui elles-mêmes impactent fortement l'intensité des glandées. Nos aménagements du modèle mécaniste confirment l'importance de ces deux processus. Des analyses complémentaires renforcent cette proposition en révélant que les dynamiques inter-annuelles de disponibilité de pollen dans l'air sont synchrones avec les dynamiques de fructification des chênes (**RS.Part_Conf 1.2),** et que la phénologie pollinique joue un rôle clé dans ces dynamiques (**RS.Part_Conf 1.3**).

Partie 1.4 : Adaptation locale du masting (Caignard *et al.* soumis, RS.Part_Conf 1.4).

Les suivis de la fructification des chênes *in situ* le long du gradient altitudinal, combinés à des tests de provenances, ont permis de mettre en évidence une forte variabilité et une adaptation locale de l'effort reproducteur entre les populations. Les observations en jardin commun révèlent une différentiation génétique entre les populations du gradient altitudinal : les populations de haute altitude allouent plus de ressources à la reproduction alors que les populations de basse altitude favorisent la croissance. Toutefois, ce cline génétique ne contrebalance pas les effets environnementaux (basses températures et gels précoces) qui limitent drastiquement la reproduction en altitude.

PARTIE 2: MASTING, DEMOGRAPHIE DES ONGULES, DEGATS AGRICOLES ET REGENERATIONS FORESTIERES

Partie 2.1: Consommation des glands par les sangliers (ONCFS)

La disponibilité en fructifications forestières semble déterminante dans l'acquisition de ressources par le sanglier, d'après l'analyse des contenus stomacaux ou fécaux (Fig. 3). En effet, si le sanglier a une alimentation essentiellement végétale, celle-ci s'avère particulièrement riche en fruits forestiers, ceux-ci pouvant constituer l'essentiel de la consommation mensuelle moyenne lors des années de forte production fruitière. En l'absence totale ou partielle de telles fructifications, l'alimentation du sanglier repose soit sur les zones de culture, soit sur les zones d'affouragement mises à disposition par les chasseurs (consommation de maïs, Fig. 3).

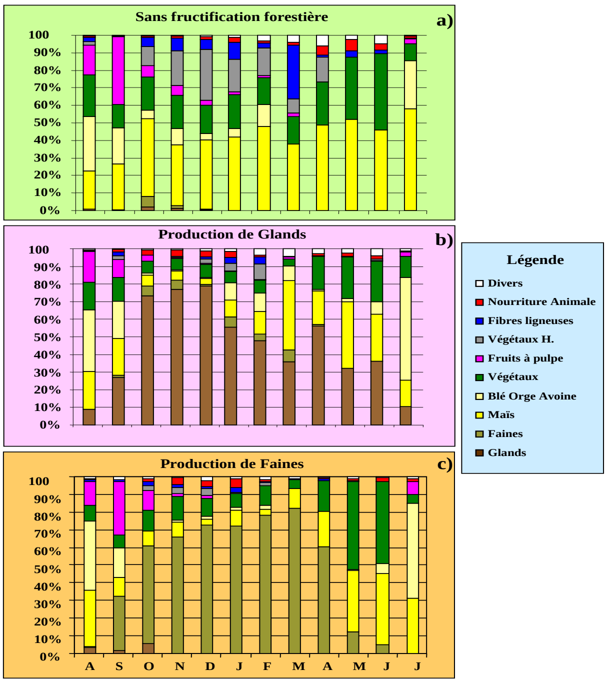

Figure 3. Composition mensuelle moyenne du régime alimentaire du sanglier en fonction des années caractérisées a) par une absence de fructification (moyenne sur 7 ans), b) par une forte glandée (moyenne sur 8 ans), c) par une forte fainée (moyenne sur 7 ans).

Partie 2.2: Impact du masting du Chêne sur la démographie des sangliers en Italie (CNR-Italie-, LBBE)

The Preserve of Castelporziano is a 60 km^2 study area located near Roma, Italy. The environment is a typical Mediterranean forest, characterized by dry summers and rainy autumns. Since 1995 a long-term monitoring program relative to the four species of ungulates living there (roe deer, *Capreolus capreolus italicus*, red deer (*Cervus elaphus*, fallow deer, *Dama dama*, and wild boar, *Sus scrofa majori*) has been carried on. Monitoring was based on nocturnal distance sampling performed in autumn for estimating population size and on capture-mark-recapture for survival estimates and, when coupled to observations on foraging sites, to estimate wild boar population at weaning time (end July). Further, we recorded body mass and reproductive traits of females shot on hunting. Acorn availability in the main habitats was estimated by placing seed traps, which were checked monthly.

In the context of PotenChêne, a specific analysis on carry-over is going to be developed. Carry over occurs when events and processes occurring one season affect individual performance in a subsequent period. Such process is widespread, but few studies on this topic have been yet performed on mammals. More specifically, we aim to investigate time-delayed effect of masting on the rate of population growth of wild boar. Path analysis allowed us to show an indirect effect on litter size and a strong impact of masting on piglet survival (Fig. 4). Albeit linear relationship was fitted between survival and masting level, it is quite likely that it exists a mast threshold in (around 15-20 for the mast index) that discriminates poor and rich years. The manuscript has to be improved by carrying out a similar analysis in another site of the PotenChêne network, namely Châteauvillain-Arc-en-Barrois (France) for which similar data are also available. This would allow to contrast two different environments and improve reliability of our findings.

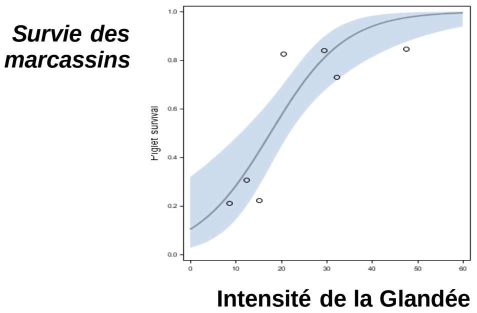

Figure 4. Survival of piglets plotted against the index of mast production. The table of statistics shows that this effect is highly statistically significant, while the effect of summer drought on survival is not detectable.

Partie 2.3: Allocation dans la reproduction: analyse comparative de deux populations de sanglier exploitant une ressource pulsée (ONCFS, CNR-Italie-LBBE ; Gamelon *et al.* 2017, Annexe A3)

Le sanglier est un animal opportuniste monophasique, qui ajuste son régime alimentaire aux ressources disponibles. Les productions forestières comme les glands, faines et châtaignes constituent une large part de son régime alimentaire. De précédents travaux ont permis d'identifier l'influence forte des productions forestières (et en particulier des glandées) sur la reproduction et la démographie du sanglier. Pourtant, aucune étude n´a encore identifié comment les femelles allouent les ressources disponibles à leur reproduction. Ceci est particulièrement important pour comprendre l´impact des fructifications forestières sur la reproduction de cette espèce.

Comme chez la plupart des larges mammifères terrestres, les femelles les plus lourdes tendent à avoir une fécondité importante. Il est donc essentiel de comprendre comment les ressources alimentaires sont allouées à la masse corporelle des femelles, et comment en retour cela se traduit par une augmentation de leur fécondité (i.e. effet indirect des ressources sur la fécondité). De plus, les ressources peuvent être allouées directement à la reproduction, sans nécessairement favoriser une masse corporelle importante (i.e. effet direct des ressources sur la fécondité). Identifier les mécanismes sous-jacents à l´allocation des ressources à la reproduction est un enjeu majeur.

C´est pourquoi nous avons mené une étude conjointe sur deux territoires contrastés. Ce travail compare deux populations, l´une dans le nord-est de la France soumise à une pression de chasse extrêmement forte, et l´autre en Italie soumise à une pression de chasse très faible. Ces deux sites diffèrent également dans leur composition forestière (espèces d'arbres présentes) ainsi que dans les patrons de fructification. Alors que le site en France est particulièrement riche en glands et faînes, le site en Italie présente une faible disponibilité en glands. Nous avons développé une analyse de chemin permettant de répondre aux questions suivantes: Comment la fructification en cours, et/ou celle de l'année précédente agit sur le patron de reproduction du sanglier ? Est-ce que cet effet ne s'exprime que de façon indirecte à travers une augmentation du poids des femelles ou l'intensité des fructifications peut-elle agir directement sur la reproduction (corps jaunes, taille de portée) ?

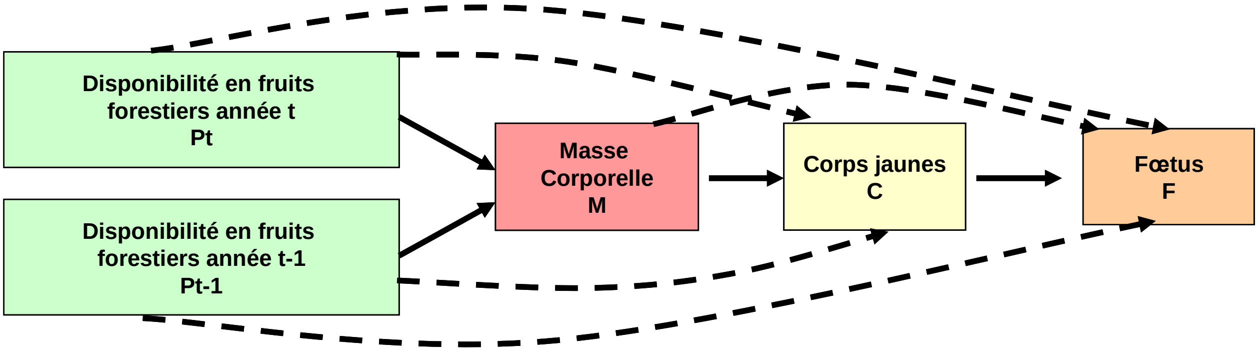

Figure 5. Schématisation de l'analyse de chemin. Le sens des flèches pleines matérialisent l'action d'un processus qui serait indirect, avec un possible effet cascade, à travers une succession de variables. Les flèches pointillées indiquent une action qui serait directe sur des variables agissant lors du processus de reproduction.

En France, seule la fructification de l'année en cours agit de manière détectable sur la reproduction. Comme attendu, cette action agit à travers un chemin indirect (Fig. 6), c'est-à-dire par le biais de la masse corporelle de la laie. Ensuite, le chemin traduit un rôle positif de la masse corporelle de la femelle sur la fertilité (qui se traduit par une augmentation du nombre de corps jaunes produits). *In fine*, la fertilité (nombre de corps jaunes) a elle-même un effet positif sur la taille de portée (qui se traduit par une augmentation du nombre de fœtus produits). À chaque étape, l'analyse permet de mesurer la force de l'effet sur le compartiment suivant. Il s'avère alors que selon le type de fructification disponible et sa quantité, l'action identifiée sera plus ou moins importante sur la masse corporelle de la laie (Fig. 6). En particulier, en France, une faînée importante une année donnée impacte plus la masse corporelle des femelles adultes qu´une glandée moyenne ou bonne. À son tour, une masse corporelle élevée favorise la fertilité et de ce fait conduits à un nombre élevé de jeunes. L´intensité des fructifications agit donc de façon indirecte sur la reproduction. Toutefois, elle agit également directement. En particulier, une bonne glandée a un effet positif sur la fertilité, et cet effet est plus marqué que celui d'une glandée moyenne, et bien plus qu'une faînée. Enfin la masse de la laie influence directement et positivement le nombre de fœtus produits (Fig. 6), indépendamment de son action sur le nombre de corps jaunes.

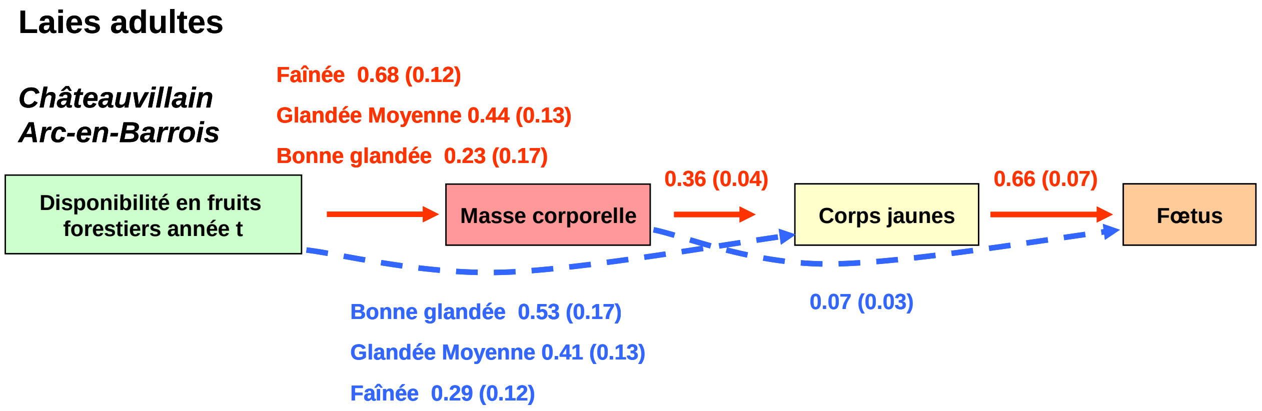

Figure 6. Résultats de l´analyse de chemin pour les femelles adultes à Châteauvillain-Arc-en-Barrois. Les flèches rouges et pleines indiquent un processus d’action indirecte des fructifications sur la reproduction, qui s’exprime à travers la masse corporelle de la femelle. Les flèches pointillées en bleu indiquent une action directe de la fructification sur la fertilité (nombre de corps jaunes produits) mais également une action indirecte de la masse corporelle sur le nombre de fœtus produits.

Contrairement à la situation observée en France, où seule la fructification de l’année en cours (année t) influence la reproduction, les fructifications à la fois de l’année en cours et de l’année précédente influencent l’ensemble du processus de reproduction chez les femelles adultes du territoire italien. Le chemin indirect se fait aussi en Italie à travers la masse corporelle de la laie. Comme en France, les fructifications des années en cours et précédente ont un effet positif direct sur le nombre de corps jaunes produits. Cependant, il s’avère aussi qu’en Italie, la fructification forestière joue un rôle direct mais négatif sur le nombre de fœtus produits, aussi bien l’année en cours que l’année précédente.

Il apparaît clairement que les laies sont capables d’ajuster leur reproduction en fonction du contexte environnemental auquel elles font face et peuvent ainsi ajuster leur effort de reproduction aux ressources alimentaires imprévisibles et fluctuantes entre années. Cette plasticité dans le processus de reproduction est un élément central des traits d’histoire de vie de l’espèce sanglier. Un travail plus détaillé et circonstancié de cette étude sera présenté dans un futur proche dans la revue Faune Sauvage.

Partie 2.4: Observatoire « reproduction du sanglier et fructifications forestières » (ONCFS)

L'Unité Ongulés de l'ONCFS (représentée par C. Saint-Andrieux et E. Baubet) a initié, en 2015, le déploiement du réseau d'observations sur la reproduction du sanglier en lien avec les fructifications forestières. Ce réseau est composé actuellement de 22 sites incluant des territoires de chasse dans 17 départements qui seront suivis pour une durée minimale de 5 ans (Fig. 7). D'autres territoires se sont portés volontaires pour rejoindre cet observatoire en 2017. L'observatoire a pour objectif de mieux connaître l'influence des productions de fruits forestiers (glands, faînes et châtaignes) estimées en fin d'été et au cours de l'automne sur le statut de reproduction des laies (classées en repos, cyclées, gestantes ou allaitantes), leur statut étant évalué au cours de la période de chasse.

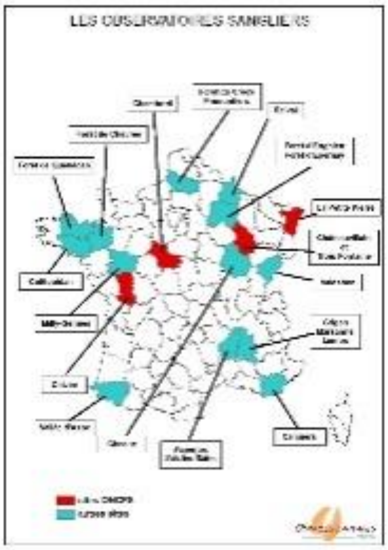

Figure 7. Les observatoires « fructification-sanglier »

Pouvoir relier le niveau des fructifications forestières (des glandées en particulier, mais aussi des productions de faînes ou de châtaignes le cas échéant) avec le niveau de recrutement annuel des populations de sangliers devrait permettre d'anticiper les mesures de gestion à prendre (dès le début de la saison de chasse) pour maîtriser les populations de sangliers. La mise en place et la gestion de cet observatoire sont assurées par le réseau Ongulés sauvages ONCFS-FNC-FDC qui implique plus largement l'ensemble des responsables des sites et les chasseurs locaux, en plus de l'équipe de recherche sanglier de l'Unité Ongulés.

Premiers résultats: Plus de 1100 tractus ont été récoltés et analysés sur l'ensemble des territoires pour la saison 2015-2016, et à peu près autant en 2016-2017. A l'échelle globale, environ la moitié des laies sont au repos, un quart sont cyclées et un quart sont gestantes. Cependant, les premières observations montrent une très grande variabilité des fructifications et des statuts reproducteurs entre les sites, et suggèrent d'ores et déjà une très forte réponse de l'allocation dans la reproduction des sangliers à l'intensité des glandées (Fig. 8).

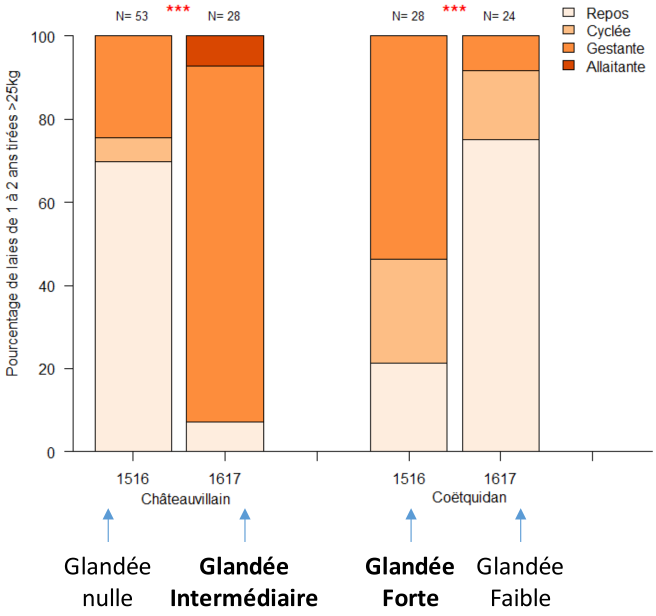

Figure 8. Statut reproducteur des laies subadultes sur deux territoires d'étude (Châteauvillain (51) et Coëtquidan (56)) au cours des deux dernières saisons (*1516* : 2015-2016 ; *1617* : 2016-2017).

Partie 2.5: Thèse de Laura Touzot, financée par la région 'Auvergne-Rhône-Alpes', à partir de novembre 2016, encadrée par le LBBE, l'ONCFS et la FNC.

Titre de la thèse: Impact du masting du chêne et du hêtre sur la dynamique des populations de sangliers dans un contexte du changement climatique: vers de nouveaux outils de contrôle des populations de sangliers.
Directeur: Jean-Michel Gaillard, **Co-encadrants**: Eric Baubet, Samuel Venner

A) Sujet de thèse

Le sanglier (*Sus scrofa*) est connu pour consommer largement glands et faînes lorsque ceux-ci sont disponibles. Cette espèce emblématique pour la chasse est en forte croissance démographique dans la plupart des pays d'Europe (prélèvements de 666 933 individus pendant la saison de chasse 2015-2016 pour le territoire métropolitain Français). Le sanglier est aujourd'hui au cœur de nombreuses préoccupations vis-à-vis des dégâts qu'il occasionne sur les cultures (identifié comme responsable de plus de 85% des dégâts occasionnés par les ongulés sur l'agriculture, le montant des indemnisations ne cesse d'augmenter et est passé de 2 à 43 millions d'euros entre 1973 et 2014 pour notre seul pays) ou bien encore des maladies qu'il échange avec les cheptels domestiques. Ces problèmes pourraient encore s'accroître au cours des décennies à venir. En effet, alors qu'en raison du changement climatique, l'intensité et la régularité des épisodes de fructifications forestières pourraient se renforcer, le taux de croissance des populations de consommateurs de ces fruits forestiers pourrait augmenter tout comme les problèmes écologiques (e.g. augmentation des densités de sangliers, effets cascades sur les espèces évoluant dans écosystèmes forestiers, diminution des capacités de régénération des forêts) et économiques qu'elles génèrent. Cependant, de nombreuses questions relatives à l'influence des fluctuations des ressources alimentaires sur la démographie (e.g. survie, croissance pondérale, fécondité, etc…) des populations de sangliers restent à explorer et pourraient permettre de contrôler durablement ces populations. L'objectif majeur de ce projet de thèse est donc de comprendre comment les ressources pulsées impactent directement les paramètres démographiques (survie, reproduction) du sanglier et plus généralement sa dynamique de population dans le contexte actuel de changements globaux, et indirectement les dégâts agricoles.

La thèse se décline selon les objectifs suivants:

(i) Valoriser les travaux qui ont été conduits pour mettre au point une méthode d'estimation légère des glandées (voir Partie 4)

(ii) Mieux comprendre le lien entre l'intensité des fructifications forestières des chênes et des hêtres, les effectifs de sangliers (estimés par les prélèvements de chasse) et l'intensité des dégâts agricoles à une échelle nationale (quasi-totalité des communes de la moitié Nord de la France) et à une échelle très locale (site d'étude de Chateauvillain - Arc en Barrois). Ce travail permettra d'inciter les gestionnaires à quantifier les fructifications (avec la méthode légère) et à adapter en conséquence les plans de chasse afin de maîtriser les pics d'effectifs engendrés par des fructifications massives. Cette approche devrait contribuer à limiter les dégâts agricoles dont les sangliers sont responsables.

(iii) Evaluer précisément l'effet des fructifications forestières sur les paramètres démographiques du sanglier, et également les effets du changement climatique sur les populations de sangliers via son effet sur le masting. Pour se faire, une version stochastique d'un modèle prédictif de la dynamique des populations de sangliers sera développée via l'intégration de données relatives aux glandées et aux faînées. Des séquences de fructifications seront ensuite simulées (i.e. variation de la fréquence et de l'intensité des pics de fructifications), afin de pouvoir prédire le bilan démographique des populations de sangliers à partir de scénarios réalistes de fructifications forestières dans un contexte de changement climatique.

B) Analyse croisée des relations entre « masting du chêne et du hêtre – prélèvements des sangliers à la chasse – dégâts agricoles » à deux échelles

Cet axe du projet vise tout d'abord à mieux comprendre le lien entre l'intensité des fructifications forestières des chênes et hêtres, la démographie des sangliers et les dégâts agricoles qu'ils occasionnent. L'hypothèse sous-jacente se décline en deux points. Tout d'abord, lors de fortes fructifications forestières, les sangliers devraient s'alimenter préférentiellement en forêt où la ressource alimentaire est abondante, et ne devraient alors causer que peu de dégâts agricoles. L'année suivante, puisque les fructifications forestières sont caractérisées par une autocorrélation temporelle négative (i.e. une année de forte production sera suivie d'une année de production faible ou nulle), les fructifications forestières devraient être faibles. Or, les effectifs de sangliers sont élevés en réponse aux conditions alimentaires favorables de l'année précédente. Par conséquent, en l'absence de fruits en forêt, ils devraient s'alimenter principalement dans les cultures voisines. L'objectif est ici de tester ces prédictions qui, si elles sont validées, devraient permettre de proposer des méthodes d'anticipation dès le printemps (grâce aux données météorologiques et de disponibilité en pollen dans l'air) des pics d'effectifs au sein des populations de sangliers et ainsi prévenir les dégâts agricoles qu'ils occasionnent.

Cet axe repose à la fois sur l'analyse de gros jeux de données disponibles sur l'ensemble du territoire français, et sur l'analyse de jeux de données de haute qualité provenant du site d'étude de Chateauvillain – Arc en Barrois (protocoles de capture-marquage-recapture déployés sur la population de sangliers et analyse des contenus stomacaux des sangliers prélevés à la chasse pour quantifier les fructifications depuis 1982). Recueillis grâce aux collaborations mises en place entre de nombreux organismes (i.e. FNC, ONCFS, IRSTEA, Météo France), ces jeux de données permettent d'avoir à la fois une vision globale et à grande échelle, ainsi qu'une vision très localisée, des relations entre les conditions météorologiques (précipitations, températures), les fructifications forestières, les effectifs de sangliers et les dégâts agricoles.

B1) Analyse à large échelle

Les données fructifications du réseau Graines et Plants ont été utilisées pour quantifier les productions de glands et de faînes. Des rayons de 10, 20 et 30 kilomètres ont été définis autour de chacun des 45 sites Graines et Plants suivis de manière continue entre 2005 et 2017 (Fig. 9). Les variables suivantes ont été estimées pour chaque site et rayon d'étude:

- moyenne mensuelle des températures quotidiennes minimales, maximales et moyennes
- production annuelle de glands et de faînes en $kg.ha^{-1}$
- pourcentage de couvert forestier pour le chêne et le hêtre
- indice de fructification relatif à la production et au pourcentage de couvert forestier
- nombre de sangliers prélevés par année à la chasse
- surface agricole détruite par les sangliers

Les analyses réalisées n'ont permis de mettre en évidence aucune relation (i) entre les fructifications forestières et le nombre de sangliers prélevés à la chasse, (ii) entre les fructifications forestières et les dégâts agricoles, ou (ii) entre les prélèvements de sangliers à la chasse et les dégâts agricoles. La non-détection de relations entre ces variables pourrait être liée à l'effet d'autres facteurs d'importance, qui ne peuvent toutefois pas être intégrés dans nos analyses. En effet, le nombre de sangliers prélevés à la chasse pourrait fortement dépendre de l'effort de chasse (e.g. nombre de chasseurs, nombre de chiens, temps passé à la chasse, etc…), l'intensité des dégâts pourrait dépendre des mesures de protection des cultures, et l'intensité des récoltes de fruits pourraient non seulement dépendre de l'intensité des fructifications mais aussi des commandes commerciales.

Lorsque nous nous intéressons aux changements des variables « nombre de sangliers prélevés à la chasse » et « surface agricole détruite par les sangliers » au cours du temps, nous constatons des cinétiques très différentes. Les effectifs de sangliers tués varient fortement d'une année à l'autre, présentant des pics de prélèvements de manière répétée dans le temps. Ce comportement n'est pas retrouvé pour les données des dégâts agricoles, qui présentent quant à elles de longues phases d'augmentation ou de diminution peut-être en lien avec les mesures de protection des cultures. Ces fluctuations des dégâts ne semblent donc pas en lien avec des dynamiques de fructification fortement variables d'une année à l'autre. Au contraire, le nombre très irrégulier de sangliers prélevés par les chasseurs pourrait quant à lui dépendre des fructifications forestières. Dans un travail en cours, nous utilisons alors une autre approche en testant la relation entre la dynamique pollinique (en lien avec la dynamique des glandées), les conditions météorologiques printanières (susceptibles d'impacter la dynamique des fructifications) et la dynamique des prélèvements de sangliers.

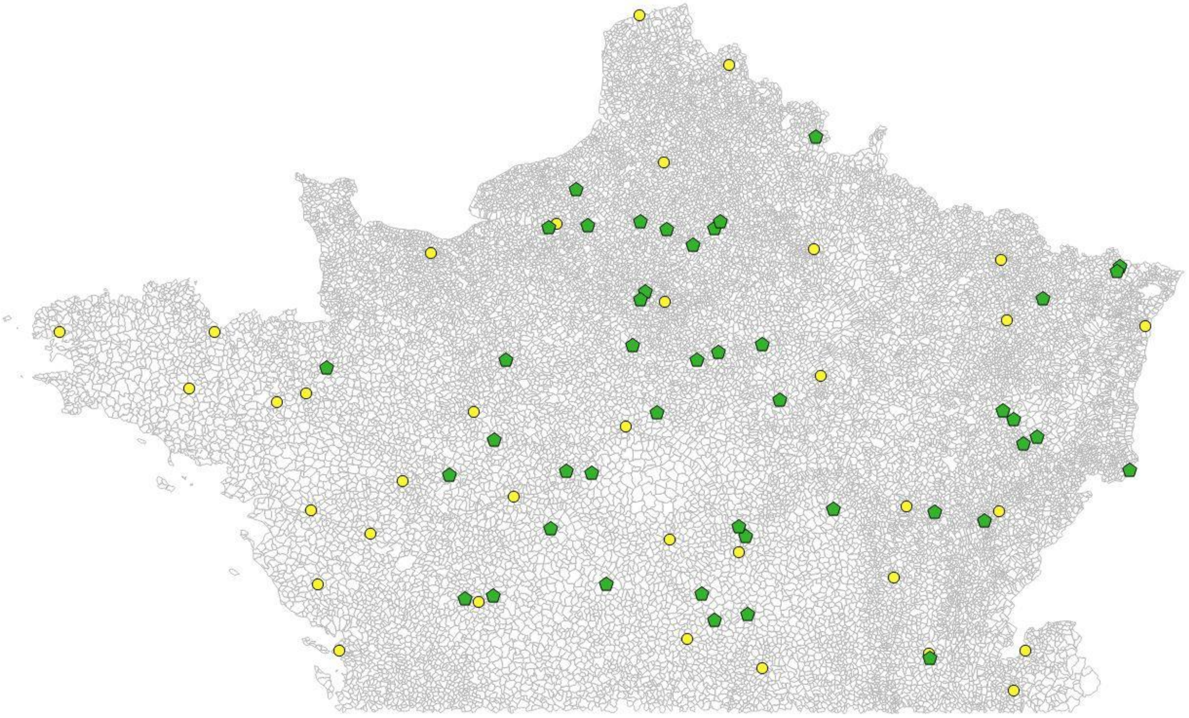

Figure 9. Localisation des sites de fructifications du réseau Graines et Plants (représentés en vert) et des sites émission de pollen du réseau RNSA (représentés en jaune) utilisés pour conduire l'analyse à large échelle.

B2) Echelle locale d'analyse

Afin d'être en mesure de comparer les tendances observées à large échelle avec celles obtenues sur un site d'étude dont nous connaissons avec précision la dynamique des populations de sangliers, nous conduirons les mêmes analyses sur le site d'étude de Chateauvillain – Arc en Barrois.

Nous pourrons dans un premier temps analyser les relations entre les données météorologiques printanières, les émissions de pollen et les fructifications forestières. Nous disposerons pour cela de deux sources de données relatives aux fructifications forestières:

- les données provenant des estomacs des sangliers tirés à la chasse

- les données provenant des protocoles d'estimation des glandées déployés dans le massif forestier

Nous serons en mesure de tester l'hypothèse que les sangliers sont opportunistes et se nourrissent principalement des ressources présentes en abondance et que les émissions de pollen combinées aux données météorologiques pourraient permettre de développer un outil de qualité pour anticiper les contenus stomacaux des sangliers et par effet de cascade, leur démographie.

Grâce aux données de capture – marquage – recapture obtenues annuellement, nous pourrons estimer de façon fiable les paramètres démographiques permettant d'obtenir une mesure de taux de croissance des populations de sangliers entre deux années consécutives. Nous pourrons ainsi tester l'hypothèse que les surfaces agricoles détruites par les sangliers dépendent de la dynamique des populations de sangliers et indirectement de la dynamique des fructifications forestières. Si tel était le cas, des anticipations de la démographie des sangliers pourraient être envisagées dès le printemps sur la base d'informations polliniques et météorologiques.

Partie 2.6: Impact des ongulés sur la régénération forestière (ONCFS, ONF ; Laurent et al. 2017, Annexe A4)

Afin d'étudier l'impact de la présence et de l'activité de 3 espèces d'ongulés (cerf, sanglier, chevreuil) sur le succès de la régénération forestière, nous avons mis en place des dispositifs expérimentaux d'enclos/exclos (Dispositif EFFORT) permettant de suivre la dynamique de la végétation (régénération forestière des chênes et du cortège floristique associé) dans une forêt de production, soit en l'absence contrôlée (enclos) soit en présence (exclos) d'ongulés, ce suivi étant réalisé depuis la coupe d'ensemencement jusqu'à l'acquisition de la régénération définitive. Le dispositif EFFORT est mis en place sur deux sites (La petite Pierre –LPP- et Trois Fontaine –TF-), la survie et la croissance des semis de chêne dans chaque enclos et chaque exclos est déterminé chaque année. Les premiers résultats montrent que la croissance des plants en hauteur y est moins rapide en exclos (Fig. 10). La confirmation de ces résultats nécessitera des observations sur plusieurs années consécutives.

Parallèlement, la probabilité de survie des semis a été estimée. Celle-ci est dépendante à la fois du facteur enclos/exclos et de l'environnement forestier (effet site :LPP vs TF), une interaction entre ces facteurs étant détectée (Fig. 11). Le taux de survie la première année est quasiment la même entre enclos et exclos quelques soit le site considéré. A partir de la seconde année, la survie en enclos devient plus élevée qu'en exclos, l'effet enclos étant beaucoup plus marqué sur le site TF que sur le site LPP. Sur le Site TF, la densité de sanglier est plus importante et le sol plus riche que sur le site LPP. Si ce résultat était confirmé, l'effet ongulés sur la régénération des chênaies serait susceptible d'être beaucoup plus marqué dans les forêts de production sur sol riche que dans les forêts se développant sur des sols plus pauvres.

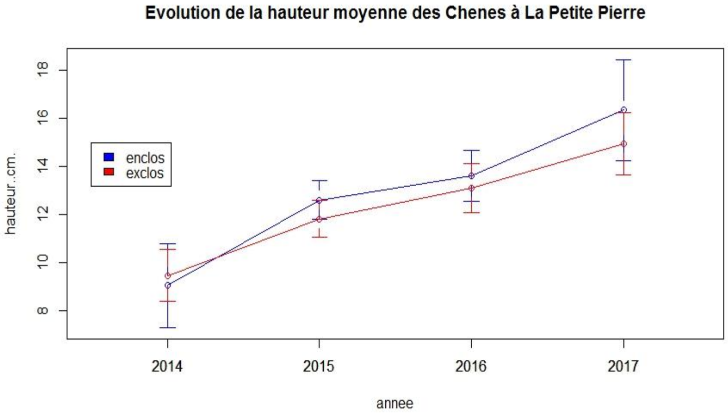

Figure 10. Croissance des jeunes plants de Chênes en enclos/exclos

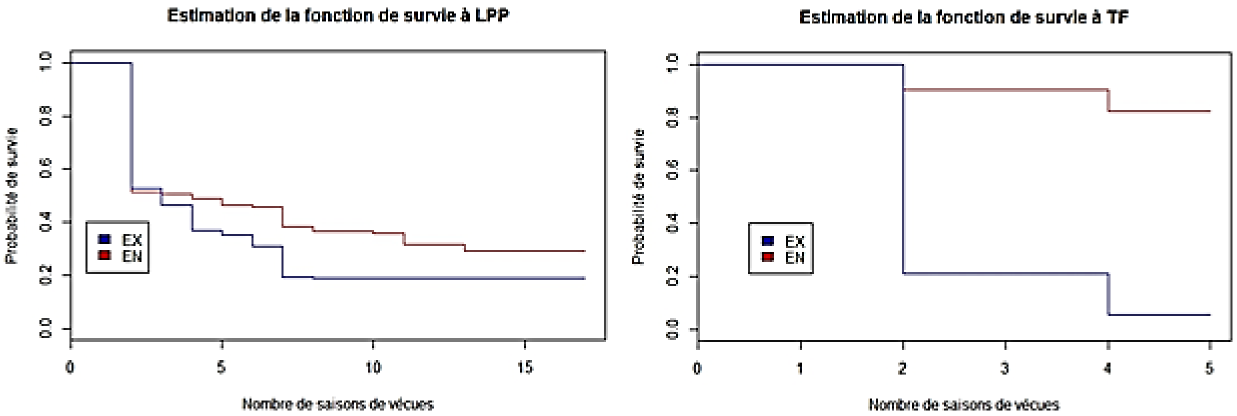

Figure 11. Estimation de la fonction de survie des semis de chêne à La Petite Pierre (gauche) et à Trois-Fontaines (droite) d'après la méthode de Kaplan-Meier.

PARTIE 3: MASTING ET DYNAMIQUE DES COMMUNAUTES D'INSECTES: UN PROBLEME DE CO-EVOLUTION (LBBE, ONF)

Les communautés d'insectes spécialistes des glands de chêne, en France, sont constituées de plusieurs espèces phylogénétiquement proches (*Curculio* spp., Coléoptères curculionidés) et d'un lépidoptère, le carpocapse (*Cydia splendana*) qui coexistent sur les mêmes arbres et qui sont en compétition pour les glands qui représentent le siège exclusif de la ponte et du développement larvaire complet. Dans cette partie, nous étudions la coévolution des stratégies des insectes et du masting (Fig. 12), la prise en compte de cette co-évolution étant probablement déterminante pour comprendre les mécanismes du masting et le devenir de la reproduction des chênes dans le contexte du changement climatique. Cette partie du programme se décline en 3 étapes et les résultats, encore non publiés sont présentés dans la partie confidentielle du rapport.

- Etude de l'impact du masting sur l'évolution des stratégies de développement des insectes (approche empirique: **RS.Part-Conf 2.1**, et approche théorique –**RS.Part-Conf 2.2**)
- Etude de l'impact des insectes sur le succès de germination des fruits, ce qui permettra d'évaluer la pression sélective que pourraient constituer les communautés d'insectes sur l'évolution du masting **(RS.Part_Conf_2.3**)
- Etude de l'évolution de la phénologie pollinique sous l'effet de la pression sélective exercée par les insectes. Ce travail visera à tester l'hypothèse que la phénologie pollinique actuelle (laquelle impacte fortement la dynamique des glandées (**RS.Part-Conf_1.1, _1.2, _1.3**) permet de générer des dynamiques de fructification avec une forte composante imprévisible et ainsi de contrôler efficacement la démographie des communautés d'insectes (**RS.Part_Conf_2.2**). Dans nos travaux à venir, nous évaluerons si, dans le contexte du changement climatique, cette stratégie de reproduction des arbres est susceptible de conserver ou non son efficacité dans le contrôle de ses consommateurs et par effet de cascade son efficacité en termes de régénération forestière.

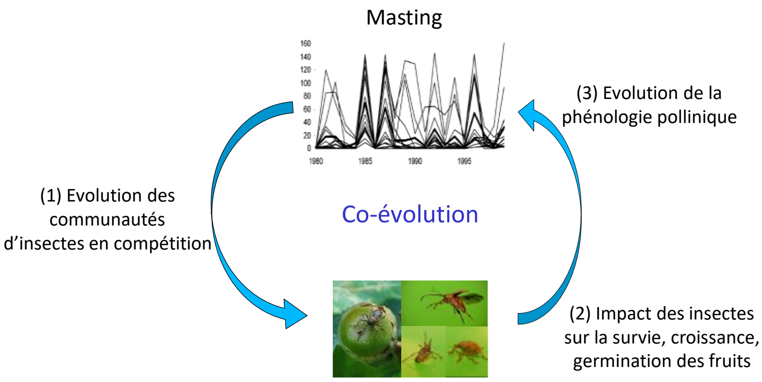

Figure 12. Étude de la co-évolution des stratégies d'exploitation des glandées par les insectes et du masting.

PARTIE 4: MISE EN PLACE D'OUTILS A DESTINATION DES GESTIONNAIRES ET SCIENTIFIQUES

Mise en place d'une méthode légère d'estimation des glandées

Les données disponibles dans la littérature qui décrivent la dynamique interannuelle des glandées reposent souvent sur une méthode de dénombrement des fruits sur arbre (un observateur posté au pied de l'arbre dénombre un maximum de glands sur un arbre en 15 secondes). Cette méthode qui, par sa légèreté, permet de suivre de nombreux arbres, est cependant fortement critiquable pour 2 principales raisons:

(1) la méthode sature vite car un observateur, même entrainé, ne peut pas dénombrer plus de 50 à 60 fruits en 15 secondes (i.e. le comptage est bridé et sous-estime les plus fortes glandées). La variabilité détectée des fructifications (entre les arbres et entre les années) sous-estimerait ainsi largement la variabilité réelle. En particulier, ces méthodes ne permettent pas de quantifier les glandées exceptionnelles en dépit des observations qualitatives récurrentes des observateurs de terrain (glandée qui peut survenir tous les 10 ans selon de nombreux témoignages d'agents de l'ONF).

(2) La méthode restreint fortement le type d'arbres et les branches éligibles (arbres qui doivent avoir des branches basses et dégagées pour assurer le comptage visuel). L'échantillonnage est fortement biaisé, notamment en milieu forestier (restreint aux arbres en lisière et aux branches basses, peu exposées au soleil) et la méthode est donc particulièrement peu adaptée aux chênaies.

En conséquence, nous avons mis en place une méthode légère de quantification des glandées basée sur le dénombrement des glands au sol (**RS.Part_Conf_3.1**). Cette méthode fournit une estimation relativement juste des glandées aux échelles de l'arbre et de la population d'arbres. Son utilisation à large échelle est d'ores et déjà envisagée pour répondre à des enjeux de gestion forestière et scientifiques.

PARTIE 5. VALORISATION DU PROGRAMME ‘POTENCHENE’

Publications scientifiques

Articles publiés

- Caignard, T., Kremer, A., Firmat, C., Nicolas, M., Venner, S., & Delzon, S. (2017). Increasing spring temperatures favor oak seed production in temperate areas. Scientific Reports, 7, 8555.
- Gamelon M., Focardi S., Baubet E., Brandt S., Franzetti B., Ronchi F., Venner S., Sæther B-E., Gaillard JM. (2017). Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. *Oecologia*, (183),1065–1076
- Laurent L, A. Mårell, P. Balandier, H. Holveck, S. Saïd. Understory vegetation dynamics and tree regeneration as affected by deer herbivory in temperate hardwood forests. 2017. Iforest, vol. 10, pp. 837-844
- Venner S., Siberchicot A. Pélisson P-F, , Schermer E, Bel-Venner M-C., Nicolas M, Débias F, Miele V, Sauzet S, Boulanger V, and Delzon S (2016) Fruiting Strategies of Perennial Plants: A Resource Budget Model to Couple Mast Seeding to Pollination Efficiency and Resource Allocation Strategies. *The American Naturalist*, 188(1), 66–75

Articles soumis pour publication

- Schermer E., Bel-Venner M.C., Fouchet D., Siberchicot A., Boulanger V., Caignard T., Thibaudon M., Nicolas M., Gaillard JM., Delzon S., Venner S. Fruiting pulses in oak tree populations: when pollen dynamics sets the tempo.
- L. Touzot, M-C. Bel-Venner, M. Gamelon, S. Focardi, V. Boulander, F. Débias, S. Saïd, E. Schermer, E. Baubet, J-M. Gaillard, S. Venner. The ground plot method: a valid and reliable assessment tool for quantifying seed production in oaks.
- Caignard T., Kremer A., Bouteiller X., Parmentier J., Louvet JM., Venner S., Delzon S. Counter-gradient variation in reproductive effort of a broadly distributed temperate oak (Quercus petraea).

Articles en phase de rédaction (soumission prévue courant 2018)

- Bel-Venner M-C *et al.* Time partitionning of a pulsed-resource exploitation and divergent evolution of morphological characters within insect communities.
- Fontanilles A., et al. On the synchrony between pollen and fruit dynamics in temperate oak populations
- Schermer E., et al. Divergence of pollen phenology among oak species and its implication in fruiting dynamics.

Articles de vulgarisation scientifique ou à destination des gestionnaires

- Durante S. Hamann JL, Baubet E, Said S. Mais où vont donc les sangliers de La Petite Pierre ? Info Chasse. Août 2015.
- Gamelon M, Focardi S, Baubet E, Brandt S, Franzetti B, Ronchi F,Venner S, Sæther B-E, Gaillard J-M. 2018. Quelle reproduction pour quelle fructification chez le sanglier. Lettre d’information du réseau « Ongulés sauvages » n°22; pp : 14-15.
- Saint-Andrieux C., 2017 - L'observatoire reproduction du sanglier et fructification forestière après un an de mise en place. Lettre d'information n° 21. P 8-11
- Saint-Andrieux C, Barthel L. 2018. L’observatoire reproduction du sanglier et fructification forestière ; bilan de deux années de suivi. Lettre d’information du réseau « Ongulés sauvages » n°22; pp : 10-13.
- Schermer E., V. Boulanger, S. Delzon, S. Said, B. Guibert, J-M. Gaillard, S. Venner. Fluctuations des glandées chez le Chêne : Mieux les comprendre pour mieux anticiper la régénération ? 2016a, Rendez-vous Technique de l’ONF n°50, p 21-29.
- Schermer E., V. Boulanger, C. Saint-Andrieux, S. Delzon, S. Said, B. Guibert, J-M. Gaillard, S. Venner. Fluctuations des glandées chez le chêne : Mieux les comprendre pour mieux contrôler les populations d'ongulés. 2016b. Lettre Ongulés sauvages n°20, p19-21.

- Schermer E., V. Boulanger, S. Delzon, S. Said, S. Focardi, B. Guibert, J-M. Gaillard, S. Venner. Fluctuations des glandées chez les chênes : mieux les comprendre pour mieux les prévoir et anticiper leurs conséquences. 2017, Forêt Nature n°145.

- **Communications scientifiques**
  - T. Caignard, F. Routier, A. Kremer, S. Delzon. Variabilité phénotypique et génétique de l'effort de reproduction du chêne sessile (*Quercus petraea*) le long d'un gradient altitudinal. Colloque francophone PHENOLOGIE 2015 Université Blaise Pascal/INRA Auvergne Rhône Alpes, Clermont-Ferrand, 18 novembre 2015
  - T. Caignard, A. Kremer, S. Delzon. Temperature effect on mast-seeding and fructification. Task Group WG2: Seed masting modeling – EU COST PROFOUND. University of Turin, Italy, 18-20 April 2016
  - T. Caignard, A. Kremer, A. Sala, S. Delzon. Fructification of European temperate oaks along environmental gradients. Organismal Biology, Ecology and Evolution (OBEE) Seminar. University of Montana, USA, March 2017.
  - T. Caignard, A. Kremer, C. Firmat, M. Nicolas, S. Venner, S. Delzon. Increasing spring temperature favors oaks seed production in temperate area. EGU General Assembly 2017. Vienna, Austria, 23-28 April 2017.
  - E. Schermer, A. Siberchicot, M-C. Venner, S. Delzon, J-M. Gaillard, S. Venner. Resource Budget Models to study the masting phenomenon. Task Group WG2: Seed masting modeling – EU COST PROFOUND. University of Turin, Italy, 18-20 April 2016
  - E. Schermer, A. Siberchicot, M-C. Venner, S. Delzon, V. Boulanger, B. Guibert, D. Fouchet, J-M. Gaillard, F. Débias, S. Sauzet, S. Venner. Reciprocal effects of the amount of pollen released and fruiting dynamics : oak trees as a case study. Colloque international : the 6th European Symposium on Aerobiology of the European Aerobiology Society (ESA), Lyon, du 18 au 22 juillet 2016.
  - E. Schermer, D. Fouchet, A. Siberchicot, M-C Venner, T. Caignard, F. Débias, V. Boulanger, B. Guibert, J-M Gaillard, S. Delzon, S. Venner. Fruiting pulses in oak populations : Does pollen dynamic set the tempo ? Colloque national 'le Petit Pois Déridé', Plateau de Saclay, Paris, du 6 au 9 juin 2017.
  - E. Schermer, D. Fouchet, A. Siberchicot, M-C Venner, T. Caignard, F. Débias, V. Boulanger, B. Guibert, J-M Gaillard, S. Delzon, S. Venner. Quand la dynamique pollinique pilote la dynamique des fructifications des arbres forestiers : le cas du Chêne. Journée de la faculté des sciences et technologies à l'UCBL, Lyon, le 22 juin.
  - E. Schermer, A. Siberchicot, D. Fouchet, M-C. Venner, V. Boulanger, B. Guibert, J-M. Gaillard, S. Venner.. 2017. Rôle de la dynamique pollinique dans le masting du Chêne. DECRYPthèse 2016, Université Claude Bernard Lyon1. Colloque organisé par l'association DocE2M2.
  - L. Touzot, M. Gamelon, B. Guibert, S. Venner, E. Baubet, J-M. Gaillard. Peut-on prédire les dégâts agricoles causés par les sangliers grâce aux fructifications forestières ? Vers une meilleure gestion des populations. Conférence intra-universitaire, DECRYPThèse, Lyon, 2 mai 2018
  - L. Touzot, M. Gamelon, S. Venner, E. Baubet, J-M. Gaillard. How does temporal variation in masting influence trait-based of exploited populations? Wild boar (Sus scrofa) as a case study. Colloque internationale EvoDemoS, Lyon, 8 - 10 janvier 2018

- **Communication/Colloques à destination des gestionnaires**
  - S. Venner, M. Nicolas, F. Debias, MC Bel-Venner, S. Sauzet, S. Delzon, V. Boulanger. Suivi des Floraisons et Fructifications des chênes Sessiles en France métropolitaine. Colloque RENCOFOR, Senones (avril 2015)
  - V. Boulanger, M. Nicolas, S. Venner. Présentation d'une enquête visant à évaluer l'intensité des glandées au cours de 30 dernières années à l'échelle de la France métropolitaine. Colloque RENCOFOR, Senones (avril 2015).
  - Said S., Pellerin M, Michallet J, Dagneaux D. Hamann JL 2015. Des ICE pour fixer les plans de prélèvements dans la RNCFS de La Petite Pierre, colloque " vers une nouvelle gestion du grand gibier : les Indicateurs de Changement Ecologique, 20-21 Mai Chambord.
  - Marell A. et Said S. 2015. Que peut nous dire la flore sur les effets des ongulés sauvages? colloque " vers une nouvelle gestion du grand gibier : les Indicateurs de Changement Ecologique, 20-21 Mai Chambord.
  - Boulanger V. et Said S. 2015. Les comparaisons Enclos-Exclos. colloque " vers une nouvelle gestion du grand gibier : les Indicateurs de Changement Ecologique, 20-21 Mai Chambord.
  - Venner S. (2016). « Potentiel de régénération des chênaies dans le contexte du changement climatique: Quel avenir pour le masting et les consommateurs de glands ? ». Séminaire conjoint REACCTIF (REcherche sur l'Atténuation du Changement ClimaTique par l'agrIculture et la Forêt) et BGF (Biodiversité, Gestion forestière et Politiques Publiques), mars 2016, Paris
  - Venner S. Comprendre les fortes variations des glandées et leurs effets sur la biodiversité associée. Colloque ‘RENECOFOR’ : 25 ans de suivi des écosystèmes forestiers, bilan et perspectives (octobre 2017, Beaune).
  - L. Touzot, M. Gamelon, S. Venner, E. Baubet, J-M. Gaillard. Impact du masting du chêne et du hêtre sur la dynamique des populations de sangliers. Rencontre MédiSanglier, Montpellier, 28 novembre 2017
  - E. Schermer, M-C. Venner, D. Fouchet, A. Siberchicot, V. Boulanger, T. Caignard, M. Thibaudon, M. Nicolas, J-M. Gaillard, S. Delzon, S. Venner. La dynamique pollinique donne-t-elle le tempo ? Séminaire RDI ONF – 8 décembre 2017.

- **Mémoires de Master 2**
  - E. Schermer. Vers une théorie unifiée du masting: analyse de l’impact des conditions climatiques sur la pollinisation combinée à la révision des modèles mécanistes du masting. 2015. Rapport de Stage de Master 2 « Modélisation en Écologie », Univ. Rennes 1 (Dir. S. Venner, V. Boulanger)
  - A. Confais. (LBBE). Divergence allométrique entre espèces d’insectes en compétition pour une ressource pulsée. 2015. Rapport de Stage de Master 2 « Ecologie comportementale, évolution et biodiversité », Univ. Tours. (Dir. S. Venner, D. Fouchet)
  - J. Froissard (LBBE) Impact de quatre espèces d’insectes du genre Curculio sur le succès de développement et de germination des glands de chênes (Quercus petraea & Quercus robur). 2016. (Dir. S Venner)
  - M. Repelin (LBBE). Ressource pulsée et coexistence d’espèces compétitrices : impact du masting des chênes sur la dynamique des communautés d’insectes consommateurs de fruits. (Dir. S. Venner ; D. Fouchet).
  - Maeva Repelin (LBBE). Ressource pulsée et coexistence d’espèces compétitrices : impact du masting des chênes sur la dynamique des communautés d’insectes consommateurs de fruits. (Dir. S. Venner ; D. Fouchet).
  - C. Rouet (LBBE). Species coexistence in fluctuating environments : Modeling the dynamics of a community in competition for a pulsed resource (Dir. S. Venner ; D. Fouchet).
  - C. Saba (ONCFS). Influence à court terme des populations d’ongulés sur la régénération forestière du Chêne et la diversité végétale (Dir. S. Saïd).

- **Memoires de stage (IUT, Licence et Master1)**

- F. Routier. Variabilité phénotypique et génétique de l'effort de reproduction le long d'un gradient altitudinal. 2015. Rapport de stage Licence III, Université de Bordeaux (Dir. S. Delzon).
- R. Sikcik. Etude de l’effet indirect des glandées sur les dégâts agricoles occasionnés par les sangliers. 2015. Rapport de stage Master 1, Univ. Lyon1. (Dir. C. Bonenfant)
- N. Wattiez. Analyse des estimateurs du masting issus d’un modèle mécaniste et comparaison avec les données empiriques. 2015. Rapport de stage Master 1, Univ. Lyon1. (Dir. S. Venner)
- N. Koenig. Causes proximales du masting du Chêne : quand la floraison ou la fructification échouent-elles ? Rapport de stage de licence 3, Univ. Lyon1. (Dir. S. Venner)
- Q. Ganivet. Impact de différentes conditions météorologiques printanières sur les dynamiques des glandées simulées. 2017. Rapport de stage de licence 3, Univ. Lyon1. (Dir. S. Venner)
- S. Monnier. Analyse de l'impact des émissions polliniques du chêne sur la démographie des populations de sangliers. 2016. Rapport de stage de 2ème année d'IUT, Lyon1. (Dir. S. Venner & C. Bonenfant).
- N. Combet. Stratégie de floraison et de fructification des chênes sessiles (*Quercus petraea*). 2016. Rapport de stage de 2ème année d'IUT, Lyon1. (Dir. M-C. Venner & S. Venner).
- S. Durante 2015 Étude des déplacements et des modes d’occupation de l’espace des sangliers (*Sus Scrofa*, L.), ainsi que les effets des variables environnementales (chasse notamment) sur ces déplacements, dans la Réserve Nationale de Chasse et de Faune Sauvage de La Petite-Pierre (Bas-Rhin).rapport de 2ème année AgroParis Tech (Dir. S. Said & E. Baubet).
- B. Varnier 2017 Observation de l’impact des ongulés sur la diversité et la régénération forestière dans la forêt d’Arc en Barrois (52) Rapport de stage de M1 (Dir. S. Said)

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Increasing spring temperatures favor oak seed production in temperate areas

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The changes in reproductive phenology (i.e. timing of flowering and fruiting) observed in recent decades demonstrate that tree reproduction has already been altered by climate change. However, understanding the impact of these changes in reproductive success and fitness remains a major challenge for ecologists. We describe here a previously unreported phenomenon: a significant increase in the reproductive effort (seed production) of temperate oaks with increasing spring temperature, observed over the last decade. In contrast, no relationship was found between seed production and precipitation. This sensitivity of seed production to temperature was confirmed by a "space-for-time" substitution based on elevation gradients. Our findings suggest that global warming may enhance oak reproductive effort in temperate ecosystems. Nevertheless, while fitness can be enhanced by higher levels of seed production, it also depends on the frequency and synchronization of mast seeding production, which may also be influenced by climate change.

Forests are important for biodiversity and as a terrestrial carbon sink[1], and contrasting responses to climate change have been identified. For instance, growth and survival, two of the main components of tree fitness, have been found to be substantially altered by climate change[2,3]. In cold and mild areas, such as boreal and temperate forests, global warming is extending tree growing seasons[4,5] and promoting wood production and tree growth[3], whereas, in warmer and drier areas, negative impacts on tree growth[6] and survival[7,8] have been observed. In addition to the reported impact on growth, and, to a lesser extent, forest dieback, we need to know how tree reproduction, one of the most important components of plant fitness, is being affected by climate change, and its likely response.

Reproduction is critical for the maintenance and demography of populations, and should therefore be assessed carefully when modeling population responses to climate change[9]. Seedling regeneration and survival are directly linked to variations in seed production[10,11] and the assessment of changes in regeneration from seeds in response to temperature has become a major challenge. There is, therefore, an urgent need to assess the impact of climate change on tree reproduction, to improve our understanding of the likely effects of this phenomenon on tree population dynamics.

An impact of climate change on the timing of reproduction has been reported for numerous organisms[12,13]. Indeed, reproductive phenology is known to be sensitive to environmental cues, such as temperature[14,15], so climate change is likely to alter the intensity of seed production. However, the impact of climate change on reproductive effort is difficult to quantify, particularly in forest trees, which display the synchronized, intermittent production of large amounts of seeds. This phenomenon, commonly observed in oak species at the population scale, is called "masting" or "mast-seeding"[16,17]. Most studies of tree seed production over long time series have focused on single sites or small numbers of sites in limited areas. The specific features of masting have, thus, made it difficult to assess the sensitivity of seed production to temperature. Moreover, as pointed out by Crone and Rapp[18], the large numbers of isolated studies and of weather variables tested have highlighted contradictory correlations with seed production, even for related species. As a result, to avoid artifacts caused by masting, the monitoring of seed production should be replicated in space and time, in ecologically independent forests.

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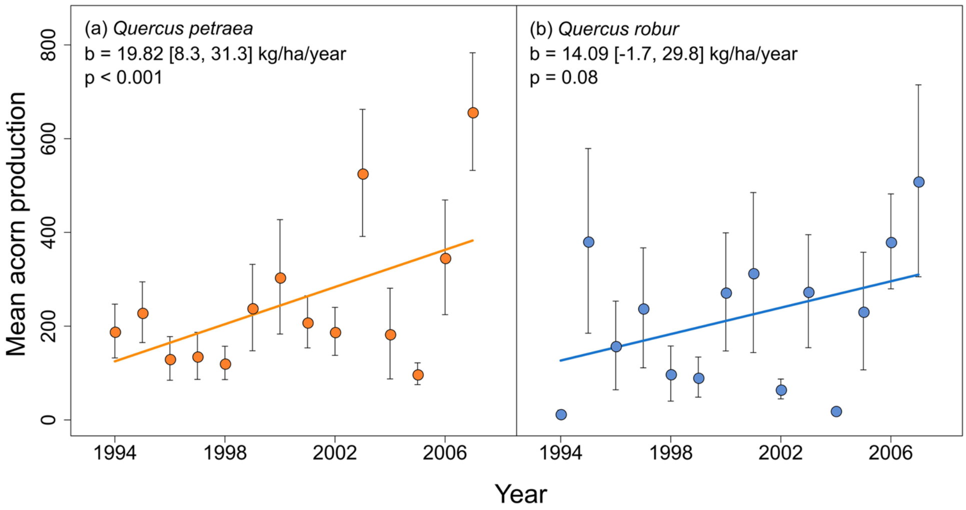

Figure 1. Temporal variation in seed production for *Quercus petraea* and *Quercus robur*. Temporal variation in seed production (kg/ha) of 19 and 9 populations of *Q. petraea* (**a**) and *Q. robur* (**b**) respectively, monitored over 14 years and distributed throughout France. Each dot corresponds to the mean seed production across all populations per year (kilograms per hectare per year averaged over all sites), the standard errors are indicated for each dot. The slope of the regression line and its 95% confidence interval, calculated from a linear mixed-effects model [2], are given for both species, with the coefficient of determination (R^2) between model [2] and mean production.

Species	**Temporal**		**Spatial**	
	M_{Acorns}/Year	**$M_{Acorns}/T_{Ap\text{-}Ma}$**	**M_{Acorns}/Alt_{100m}**	**$M_{Acorns}/T_{Ap\text{-}Ma}$**
Q. petraea	**19.82 [8.3, 31.3]**	**111.89 [63.1, 146.0]**	**−83.89 [−149.5, −18.3]**	**334.2 [175.6, 589.2]**
Q. robur	14.07 [−1.7, 29.8]	**72.66 [19.6, 120.5]**	—	—

Table 1. Temperature sensitivity of reproductive efforts in oaks. Slopes of the linear mixed-effect regression between acorn production in kilograms per hectare (M_{Acorns}) and year (temporal gradient, (M_{Acorns}/Year)), and for every 100 m increase in elevation (spatial gradient, M_{Acorns}/Alt_{100m}), and the mean temperature in April and May in °C ($M_{Acorns}/T_{Ap\text{-}Ma}$) in both studies. The 95% confidence intervals are indicated in square brackets. Reproduction in *Quercus petraea* was monitored in both studies, whereas *Quercus robur* was monitored in the temporal gradient study only. Significant correlations are indicated in bold.

In this study, we analyzed extensive sets of tree reproduction data for two temperate European white oak species (the sessile oak (*Quercus petraea*) and the pedunculate oak (*Q. robur*)), to determine whether seed production had changed over the last two decades in response to global warming. Seed production was monitored in 28 forests of *Q. petraea* and *Q. robur* distributed throughout France over a period of 14 years. In parallel, a "space-for-time" substitution was used to quantify the temperature sensitivity of acorn production over elevation gradients. These analyses demonstrated significant temperature-induced trends in seed production over the last two decades, suggesting that climate change enhances oak reproductive effort in temperate ecosystems.

Results and Discussion

Temporal trend in seed production. We examined temporal changes in the seed production of two oak species across France over recent decades (1994 to 2007) (Figure S1). We observed an increase over time in reproductive effort for both species (Fig. 1). On average, acorn production (M_{acorn}) in *Q. petraea* populations increased by 19.8 [8.3, 31.3] kg/ha/year (Table 1) and by 14.1 [−1.7, 29.8] kg/ha/year for *Q. robur*. However, for *Q. robur* the regression slope was not significant (Table 1). In addition, the effects of age and diameter have been tested and are reported in Table S1. For both species, growth does not help to explain the variation in seed production (Table S1). However, aging had a significant negative effect on the fructification of *Q. petraea* (Table S2) while no effect was found for *Q. robur*. Such a negative effect suggests that older *Q. petraea* populations produce less acorns than younger ones. This strengthens the positive trend in seed production observed over time. Similar positive temporal trends have been reported in a few other studies. A limited number of reports for *Pinus engelmannii*[19] and in *Nothofagus solandri*[20, 21] have demonstrated temporal shifts. In these studies, the monitored populations were located at high elevations, at which reproduction appears to be more sensitive to environmental change[20, 21]. However, in most cases, no temporal trend in fruit production, for example, was observed[22, 23] and such trends have rarely even been sought, due to the scarcity of adequate, long-term datasets. In our study, the many populations surveyed were found in temperate lowland forests located over a large area and at an elevation of between 55 and 330 m above sea level. The mean synchrony of seed production (Spearman correlation coefficient) among the

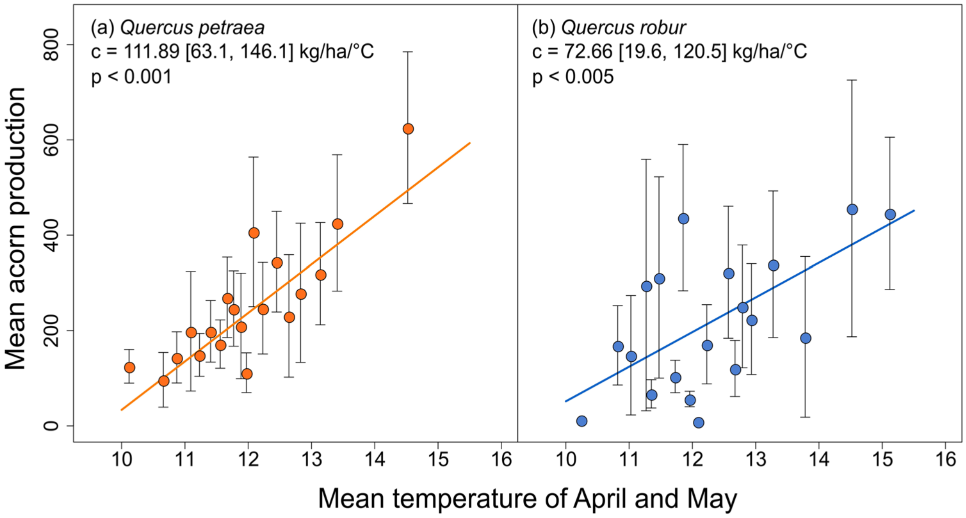

Figure 2. Responses of seed production to spring temperature for both *Quercus petraea* and *Quercus robur*. Changes in acorn production per population and per year (M_{Acorns}) for *Q. petraea* (**a**) and *Q. robur* (**b**) according to mean spring temperature. For both species, acorn production data for all populations and all years were binned into 19 temperature classes of approximately the same size, 14 for *Q. petraea* and 6 or 7 for *Q. robur*. Mean acorn production per bin is correlated with the temperature class median, the standard errors are indicated for each dot. The slope of the regression line and its 95% confidence interval, calculated from a linear mixed-effects model [4], and the coefficient of determination (R^2) between the model [4] and the binned data are given for each species.

populations was very low for both species (0.11 ± 0.016 for *Q. petraea* and 0.15 ± 0.052 for *Q. robur*), demonstrating the lack of synchrony between populations over this large scale (the differences in seed production dynamics between the populations monitored are shown in Figure S2). It is worth noticing that the degree of synchrony changes according to the distance between populations, explaining the low overall synchrony over the large distribution of the populations monitored in our study: the greater the distance between two populations is, the lower the synchrony (Figure S3). As the populations were independent, any common temporal change in reproductive effort can be seen as a robust overall pattern rather than a local trend in a marginal population. Many studies have explored the potential drivers of plant reproduction[18, 24, 25], but only a few have investigated changes in reproductive effort in response to global warming, due to a general lack of statistical power[26, 27]. The large number of asynchronous populations monitored in our study provides a significant advance to assess changes in reproduction though time and according to temperature. In the context of climate change, the temporal trends observed here may reflect the effects of recent warming over the last few decades. Consistent with this view, we observed a significant increase in temperature over time at the sites studied (Figure S4), potentially sufficient to account for the positive temporal trend observed.

Reproductive effort in oak is increasing with increasing spring temperatures in temperate areas. Temperature and rainfall are routinely recorded and are considered the most relevant climatic variables driving seed production[24], but their effects seem to differ between tree species and ecosystems[23]. Tree reproductive effort has been studied mostly in Mediterranean oak species and monitored mostly in Southern Europe and California[28]. For most of the Southern European species, a warmer, drier summer season results in lower levels of seed production[29, 30]. Interestingly, the main driver appears to be water deficit rather than temperature *per se*[31, 32]. By contrast, we found that, in both *Q. petraea* and *Q. robur*, seed production was positively correlated with spring temperature (Fig. 2a,b and Table 1), which is known to have a strong effect on flowering and pollination[14, 15]. Moreover, no correlation was found between seed production and annual or seasonal precipitations (Table S3). No study has ever reported positive temporal clines for acorn production, but positive correlations with spring temperature have been found in California for three Mediterranean oak species, *Q. lobota*, *Q. douglasii* and *Q. kelloggii*[33], and three temperate oak species, *Q. alba*, *Q. rubra* and *Q. velutina*[17]. In our study, despite the broad distribution of the populations, the positive correlation with spring temperature observed could be explained mostly by temperature variability over time rather than temperature variability over space (Table S4). The trend towards an increase in seed production over time observed for both species was therefore directly correlated with the increase in spring temperature observed over the last decade (Figure S4). Climate change has had a negative impact on reproduction in Mediterranean oaks in Europe[32, 34], but we show here that the increase in spring temperature has favored reproduction in temperate oaks. Such a difference could be explained by a water scarcity threshold that is annually reached in Mediterranean ecosystems, while precipitation is currently not limiting for reproduction in European temperate ecosystems.

We then examined seed production along elevation gradients in Southern France, to refine the temperature-seed production relationship. Our findings confirm the strong positive correlation between seed production and spring temperature in *Q. petraea* (Table 1). The gain in acorn production per one-degree rise

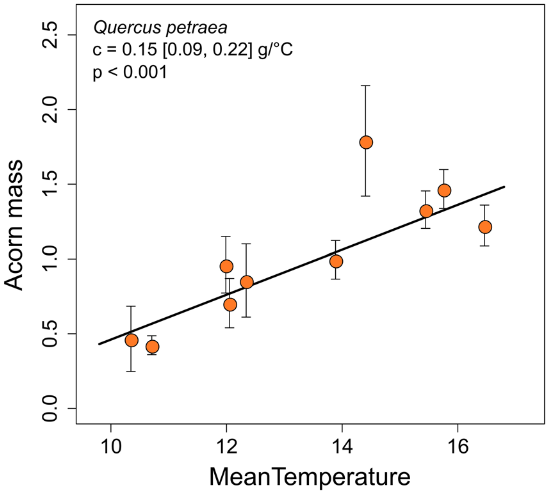

Figure 3. Temperature trends in seed mass for *Quercus petraea*. Trend in acorn mass (g) with mean temperature from April to November (°C) along the elevation gradient. Each dot corresponds to the mean acorn mass, across years and trees, per population along the elevation gradients. The slope of the regression line and its 95% confidence interval, calculated from a linear mixed-effects model, and the coefficient of determination (R^2) are indicated. April to November corresponds to reproductive cycle length in *Q. petraea*: from flowering to acorn release.

along the elevation gradient ($M_{acorn}/T_{Ap\text{-}Ma} = 334.2$ kg/ha/°C) was three times greater than that along the spatio–temporal gradient ($M_{acorn}/T_{Ap\text{-}Ma} = 111.89$ kg/ha/°C). This difference may reflect differences in temperature values and gradients between the two designs. Indeed, the range of spring temperature variation was lower for the spatio-temporal gradient (6.2 °C) than for the elevation gradient (10.8 °C).

What is the impact on tree fitness?. Our observations suggest that climate change may increase the fitness of temperate oaks. An increase in seed production is beneficial to the tree, as it increases seed dispersal[35, 36], thereby increasing the number of potential offspring and, consequently, their establishment. In addition, acorn mass increases with increasing temperature, by about 0.15 g per degree [0.09, 0.22] (Fig. 3). This gain may increase the resistance of acorns to environmental stress (predation by insects, frost) and enhance germination[37, 38]. However, reproduction in many tree species, including oaks, is characterized by masting or mast-seeding, with synchronized large-scale seed production at the population scale (Figure S2). This process is considered to be an adaptive response to the selective pressure exerted by predators[16, 17]. Masting limits seed predation and promotes seed dispersal, thereby ensuring high rates of offspring survival and optimizing resource allocation to reproduction[24, 39]. Changes in masting associated with climate change may, therefore, have a negative impact on the fitness of tree populations.

Nowadays climate change effect on masting frequency is still uncertain and only few studies have investigated change in masting frequency and long-term shifts in allocation to seed production. For instance, Övergaard *et al.*[40] observed, during 30 years of measurement in European beech forest (*Fagus sylvatica*), an increase in the frequency of mast events directly correlated with an increase in temperature. With increasing periodicity, the temporal variability characterizing mast-seeding and enabling the trees to control predator population size[24, 41] might be greatly reduced[27]. Low inter-annual variability in seed crops may lead to an increase in predator population size, decreasing reduce offspring survival. This paradoxical consequence of climate warming for temperate tree reproduction highlights the need for improvements in our understanding of the proximal mechanisms underlying masting in trees, for prediction of the response of forest ecosystems to climate change.

This study focused on temperate forests dominated by deciduous oak species and cannot be extended to other forest types. However, we can compare the time and temperature trends of acorn production observed in oaks with the patterns reported for whole biomass growth in trees[42, 43]. There is a clear congruent increase in vegetative growth and reproductive growth (our results) in *Q. petraea* and *Q. robur* in recent decades in central Europe. Such trends can be seen as two facets of the overall consequence of the same causes relating to global changes in recent decades. An increase in temperature extends the period of vegetative growth[4, 5] and enhances tree growth[44]. In addition to increasing temperature, increases in the carbon dioxide content of the atmosphere may also promote tree growth in some species, and increases in nitrogen (N) deposition have been shown to stimulate forest growth and carbon sequestration in Europe[45]. As reproduction in trees is also dependent on resource availability[46–49], the combined effects of temperature, carbon dioxide, and nitrogen deposition may also contribute to the increase in seed production. Despite a likely competition for resources between these two processes, a concurrent increase in both is reliable as there seem to be largely independent of each other[50]. However, the congruent pattern of vegetative and reproductive growth may be negatively affected by extreme events and disturbances, such as firestorms or the spread of insects and diseases, which may also be triggered by global changes[51].

Global warming has had a positive effect on temperate oak growth. However, the response of tree reproduction to environmental changes remains unclear, mostly due to our limited understanding of masting processes. Long-term studies of reproductive investment over large areas would be required to assess the global impact of climate change on trees.

Material and Methods

Study sites. We analyzed variations in seed production for two European oak species (Quercus petraea and Quercus robur) along a latitudinal and an elevation gradients. The latitudinal field survey is made of 28 permanent plots that are part of the French intensive forest monitoring network (RENECOFOR) (Figure S1). These plots are widely distributed across France, between latitudes of 43.2° and 50.2°N and longitudes of 0.04° and 3.7°E (Table S5). They correspond to oak tree populations dominated by *Q. petraea* for 19 of them and by *Q. robur* for the 9 other ones. All of these populations were already mature when they started to be monitored (mean age of 85.5 years ± 28.7 in 1994). Seed production was assessed for 14 years, from 1994 to 2007. Due to a budget cut, the monitoring program stopped after 2007 and no data of fructification were available after this date. In each forest plot, acorns were collected at the population scale, with ten 0.5 m^2-litterfall traps set up under the closed canopy and evenly distributed over an area of about half a hectare. The litter fallen into the traps was collected each season, and sorted by distinguishing the leaves, branches and acorns from oak trees. Acorns were then separated from their cupule and oven-dried. The dry mass of acorns was measured, then divided by the total area of all the traps and expressed in kg/ha. In addition, the mean diameter of trees in each population were assessed every five years from 1991 to 2014. We then estimated it every year using linear regressions. Daily mean, minimal and maximal temperatures (°C) and precipitation (mm) were extracted from the SAFRAN[52] spatially explicit database (8 × 8 km grid) for each site.

The elevation gradient survey was set up in the French Pyrenees, along a replicated transect in two parallel valleys: Ossau and Gaves (latitude 42°47′N to 43°45′N; longitude 00°44′W to 00°06′E). Five natural mature populations of *Q. petraea* were monitored in each valley, at different elevations, from 131 m to 1630 m (Table S5). At each site, nets were set up 1 m above the ground under the whole tree canopy, to collect all the acorns produced by an individual. In total 15, 13, 25 and 30 adult trees were monitored in 2012, 2013, 2014 and 2015, respectively. The 30 trees had a mean height of 19.2 ± 9.4 m and a mean diameter of 37.7 ± 19.6 cm. From 2012 onwards, the organic components (leaves, branches, fruits) fallen from the trees were harvested every two weeks, from the end of September until the beginning of December. For each tree, the projected area of the canopy on the ground (SC_{OBi}) was calculated by first defining the canopy center (O) and then determining the distance from O to the outer limit of the canopy (B_i), at 8 points, 45° apart (OB_{1-8}). The surface area was calculated as:

$$SC_{OB_i} = \frac{\pi}{i} \times \sum OB_i^2 \tag{1}$$

The harvested litters were sorted in the laboratory, and total acorn production, total dry mass and mean acorn weight per tree and per year (g) were determined. Total seed production was normalized by dividing by the total projected surface area of the tree canopy. Air temperature was measured with a data logger (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, Massachusetts, USA) at all sites. Data were recorded hourly, from January 1 2012 to December 31 2015.

Statistical analysis. *Temporal trend.* We evaluated the change in seed production over time separately for the two species, with a linear mixed-effects model:

$$Y_{j\Theta} = a_\mu + b_\mu\Theta + (a_j + b_j\Theta) + \varepsilon_{j\Theta} \tag{2}$$

where a_μ and b_μ are respectively the overall intercept and the overall regression slope of acorn production regressed over time (Θ) a_j and b_j are the random population-specific intercept and slope deviations associated with population j,, and $\varepsilon_{j\Theta}$ are the residuals. For both species, we compared the model [2] with a simpler model not accounting for population random-deviation in slope b_j. The fit of the two models was compared with a likelihood-ratio test. No significant variation in slope were detected for both species (*Q. petraea*: $\chi^2 = 0.18$, $p = 0.91$; *Q. robur*: $\chi^2 = 0.00$, $p = 1$) indicating that the temporal trends were similar among populations (the variance of b_j did not differ from zero). Parameters were thus estimated from the simpler model: $Y_{j\Theta} = a_\mu + b_\mu\Theta + (a_j) + \varepsilon_{j\Theta}$.

In addition, we assessed change in seed production over time separately for the two species and compared linear mixed-effects models adding tree age and diameter as fixed effect to the simpler model [2]:

$$Y_{j\Theta AD} = a_\mu + b_\mu\Theta + d_\mu A + g_\mu D + (a_j) + \varepsilon_{j\Theta AD} \tag{3}$$

where d_μ and g_μ are the regression slopes of acorn production regressed respectively over the mean age of the population in 1994 (A) and over the mean diameter of the population estimated for every year (D). To determine which of the two covariates helps to explain better the variation in seed production, we compared models with and without the effects of tree age (A) and diameter (D) using the Akaike Information Criterion corrected for small sample size (AICc) (Table S1). Models with the lowest AICc were selected, however, we consider models with ΔAICc between 0 and 2 to have equivalent support[53] and based on the principle of parsimony we selected the simplest one.

For *Q. petraea*, AICc differences gave support to the model with the fixed effect $d_\mu A$, (Table S1), thus, we estimated the effect of age on acorn production (Table S2).

We then evaluated the response of seed production to temperature:

$$Y_{ijT} = a_\mu + c_\mu T + (a_j + c_j T) + \varepsilon_{ijT} \tag{4}$$

where c_μ is the general regression slope of acorn production regressed against temperature (T), a_j is the random deviation associated with population j, and c_j is the random population-specific deviation in slope, and ε_{ijT} denotes the residuals. As before, we compared the model [4] with a simpler model not accounting for population random-deviation in slope (c_j). No significant variation in slope were detected for both species (Likelihood-ratio tests: *Q. petraea*: $\chi^2 = 2$, $p = 0.08$; *Q. robur*: $\chi^2 = 2$, $p = 0.12$), indicating that the effect of temperature on acorn production was consistent among populations (Figure S5).

We therefore used the simplified model [4] (i.e. $Y_{ijT} = a_\mu + c_\mu T + (a_j) + \varepsilon_{ijT}$) to evaluate the effect of temperature on seed production. Model [4] was compared to a model without the temperature fixed effect c_μ, using the Akaike Information Criterion corrected for small sample size (AICc). To determine the temperature variable having the strongest influence on seed production, this comparison was performed taking several estimations of annual temperature *T:* the mean temperature computed for each month and the mean temperature computed for every two month over the year. AICc differences giving support to the more complex model were much higher for the periods of April (AICc = 28.1), March-April (AICc = 17.2), and April-May (AICc = 18.8), for *Q. petraea* and for April (AICc = 4.9), and April-May (AICc = 5.2) for *Q. robur* (Figure S6). As the ΔAICc were higher for temperatures recorded during the spring months, we refined the analysis to different spring periods (Table S7). For *Q. petraea*, a significant regression slope was found with the temperature in April ($c_\mu = 94.8$ [61.5, 128.4] kg/ha/°C), March-April ($c_\mu = 103.0$ [56.6, 152.4] kg/ha/°C), April-May ($c_\mu = 111.9$ [63.1, 146.1] kg/ha/°C) and May-June ($c_\mu = 41.6$ [1.1, 86.1] kg/ha/°C). For *Q. robur*, a significant regression slope was observed only for April ($c_\mu = 54.07$ [14.4, 93.7] kg/ha/°C) and April-May ($c_\mu = 72.66$ [19.6, 120.5] kg/ha/°C (Tables 1 and S7). The mean temperatures during the periods of April and April-May are determinant for seed production in both species. We represented April-May period in Fig. 2 as it covered a larger period.

To evaluate the effect of precipitation on fructification, we compared model [4] with a similar mixed effect model taking into account the sum of precipitations as a fixed effect in addition to the spring temperature. The inclusion of the five precipitation periods: winter, (January to March), spring (April to June), summer (July to September), autumn (October to December) and the whole year, as predictor were compared with model [4] using AICc.

As spring temperature was found to have increased over the last decades (Figure S4) and seed production was significantly correlated with temperature (Table 1 and Fig. 2), we considered the observed temporal trend in seed production in both species (Table 1 and Fig. 1) to be due principally to the increase in temperature. However, as the populations were distributed over a large area covering a large range of temperatures, we explicitly accounted for variability due to the year and population, with the following multiple regression model:

$$Y_{ijT_PT_Y} = a_\mu + b_\mu T_P + c_\mu T_Y + (a_j) + \varepsilon_{ijT_PT_Y} \tag{5}$$

where b_μ denotes the overall slope of the mean population temperature regressed against year (T_P) and c_μ is the overall slope of mean yearly temperature regressed against population (T_Y) for acorn production. a_j is the population random intercept and and $\varepsilon_{ijT_PT_Y}$ denotes the residuals. We used model [5], with the mean temperature of April-May (Table S4).

Trend along the elevation gradient. We then evaluated the sensitivity of reproduction to temperature along the elevation gradients in Pyrenees. We used the following mixed-effect model:

$$Y_{ijkT} = a_\mu + c_\mu T + (p_j) + (n_{k(j)}) + \varepsilon_{ijkT} \tag{6}$$

where a_μ denotes the overall intercept and c_μ the overall regression slope of acorn production against temperature (T), p_j and $n_{k(j)}$ are the random deviations associated with population j and the individuals k within population j, respectively, and the residuals are denoted ε_{ijKT}. We tested the effect of temperature over the same period as above (Tables 1 and S7).

Finally, using the same model [6], we also evaluated the sensitivity of acorn size to temperature along the same elevation gradient.

All the linear mixed effects models were fitted by the restricted maximum likelihood (REML)[54] method in the *lme4* R package[55].

References

1. Pan, Y. *et al.* A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993 (2011).
2. Anderegg, W. R. L., Kane, J. M. & Anderegg, L. D. L. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* **3**, 30–36 (2013).
3. Briceño-Elizondo, E., Garcia-Gonzalo, J., Peltola, H., Matala, J. & Kellomäki, S. Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. *For. Ecol. Manag.* **232**, 152–167 (2006).
4. Menzel, A. & Fabian, P. Growing season extended in Europe. *Nature* **397**, 659–659 (1999).
5. Vitasse, Y., Porté, A. J., Kremer, A., Michalet, R. & Delzon, S. Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia* **161**, 187–198 (2009).
6. Jump, A. S., Hunt, J. M. & Peñuelas, J. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Change Biol.* **12**, 2163–2174 (2006).
7. Allen, C. D. *et al.* A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manag.* **259**, 660–684 (2010).
8. Park Williams, A. *et al.* Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* **3**, 292–297 (2012).

9. Morin, X., Viner, D. & Chuine, I. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *J. Ecol.* **96**, 784–794 (2008).
10. Moles, A. T. & Westoby, M. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.* **92**, 372–383 (2004).
11. Turnbull, L. A., Crawley, M. J. & Rees, M. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* **88**, 225–238 (2000).
12. Fitter, A. H. & Fitter, R. S. R. Rapid changes in flowering time in British plants. *Science* **296**, 1689–1691 (2002).
13. Menzel, A. *et al*. European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* **12**, 1969–1976 (2006).
14. Sherry, R. A. *et al*. Divergence of reproductive phenology under climate warming. *Proc. Natl. Acad. Sci. USA* **104**, 198–202 (2007).
15. Hedhly, A., Hormaza, J. I. & Herrero, M. Global warming and sexual plant reproduction. *Trends Plant Sci.* **14**, 30–36 (2009).
16. Kelly, D. The evolutionary ecology of mast seeding. *Trends Ecol. Evol.* **9**, 465–470 (1994).
17. Sork, V. L. Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.). *Vegetatio* **107**, 133–147 (1993).
18. Crone, E. E. & Rapp, J. M. Resource depletion, pollen coupling, and the ecology of mast seeding: Mechanisms of mast seeding. *Ann. N. Y. Acad. Sci.* **1322**, 21–34 (2014).
19. Buechling, A., Martin, P. H., Canham, C. D., Shepperd, W. D. & Battaglia, M. A. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. *J. Ecol.* **104**, 1051–1062 (2016).
20. Allen, R. B., Hurst, J. M., Portier, J. & Richardson, S. J. Elevation-dependent responses of tree mast seeding to climate change over 45 years. *Ecol. Evol.* **4**, 3525–3537 (2014).
21. Richardson, S. J. *et al*. Climate and net carbon availability determine temporal patterns of seed production by *Nothofagus*. *Ecology* **86**, 972–981 (2005).
22. Abraham, S. T., Zaya, D. N., Koenig, W. D. & Ashley, M. V. Interspecific and intraspecific pollination patterns of valley oak, *Quercus lobata*, in a mixed stand in coastal Central California. *Int. J. Plant Sci.* **172**, 691–699 (2011).
23. Koenig, W. D. & Knops, J. M. H. Environmental correlates of acorn production by four species of Minnesota oaks. *Popul. Ecol.* **56**, 63–71 (2014).
24. Kelly, D. & Sork, V. L. Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* 427–447 (2002).
25. Pearse, I. S., Koenig, W. D. & Kelly, D. Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytol.* **212**, 546–562 (2016).
26. Kelly, D. *et al*. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecol. Lett.* **16**, 90–98 (2013).
27. Mckone, M. J., Kelly, D. & Lee, W. G. Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. *Glob. Change Biol.* **4**, 591–596 (1998).
28. Koenig, W. D. *et al*. In *Mediterranean Oak Woodland Working Landscapes* (eds Campos, P. *et al.*) 181–209 (Springer Netherlands, 2013).
29. Cecich, R. A. & Sullivan, N. H. Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*. *Can. J. For. Res.* **29**, 1817–1823 (1999).
30. Fernández-Martínez, M., Belmonte, J. & Maria Espelta, J. Masting in oaks: Disentangling the effect of flowering phenology, airborne pollen load and drought. *Acta Oecologica* **43**, 51–59 (2012).
31. Pérez-Ramos, I. M., Ourcival, J. M., Limousin, J. M. & Rambal, S. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology* **91**, 3057–3068 (2010).
32. Sanchez-Humanes, B. & Espelta, J. M. Increased drought reduces acorn production in *Quercus ilex* coppices: thinning mitigates this effect but only in the short term. *Forestry* **84**, 73–82 (2011).
33. Koenig, W. D., Knops, J. M., Carmen, W. J., Stanback, M. T. & Mumme, R. L. Acorn production by oaks in central coastal California: influence of weather at three levels. *Can. J. For. Res.* **26**, 1677–1683 (1996).
34. Pérez-Ramos, I. M., Padilla-Díaz, C. M. & Koenig, W. D. & Marañón, T. Environmental drivers of mast-seeding in Mediterranean oak species: does leaf habit matter? *J. Ecol.* **103**, 691–700 (2015).
35. Jansen, P. A., Bongers, F. & Hemerik, L. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol. Monogr.* **74**, 569–589 (2004).
36. Vander Wall, S. B. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 989–997 (2010).
37. Aizen, M. A. & Woodcock, H. Effects of acorn size on seedling survival and growth in *Quercus rubra* following simulated spring freeze. *Can. J. Bot.* **74**, 308–314 (1996).
38. Gómez, J. M. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution* **58**, 71–80 (2004).
39. Herrera, C. M., Jordano, P., Guitián, J. & Traveset, A. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *Am. Nat.* **152**, 576–594 (1998).
40. Övergaard, R., Gemmel, P. & Karlsson, M. Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* **80**, 555–565 (2007).
41. Silvertown, J. W. The evolutionary ecology of mast seeding in trees. *Biol. J. Linn. Soc.* **14**, 235–250 (1980).
42. Boisvenue, C. & Running, S. W. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Glob. Change Biol.* **12**, 862–882 (2006).
43. McMahon, S. M., Parker, G. G., Miller, D. R. & Schlesinger, W. H. Evidence for a Recent Increase in Forest Growth. *Proc. Natl. Acad. Sci. USA* **107**, 3611–3615 (2010).
44. Saxe, H., Cannell, M. G., Johnsen, Ø., Ryan, M. G. & Vourlitis, G. Tree and forest functioning in response to global warming. *New Phytol.* **149**, 369–399 (2001).
45. Magnani, F. *et al*. The human footprint in the carbon cycle of temperate and boreal forests. *Nature* **447**, 849–851 (2007).
46. Isagi, Y., Sugimura, K., Sumida, A. & Ito, H. How does masting happen and synchronize? *J. Theor. Biol.* **187**, 231–239 (1997).
47. Ichie, T., Kenzo, T., Kitahashi, Y., Koike, T. & Nakashizuka, T. How does Dryobalanops aromatica supply carbohydrate resources for reproduction in a masting year? *Trees* **19**, 704–711 (2005).
48. Hoch, G. Carbon Reserves as Indicators for Carbon Limitation in Trees. In *Progress in Botany* 321–346 (Springer, 2015).
49. Sala, A., Hopping, K., McIntire, E. J. B., Delzon, S. & Crone, E. E. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytol.* **196**, 189–199 (2012).
50. Knops, J. M., Koenig, W. D. & Carmen, W. J. Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. *Proc. Natl. Acad. Sci.* **104**, 16982–16985 (2007).
51. Seidl, R., Schelhaas, M.-J., Rammer, W. & Verkerk, P. J. Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Change* **4**, 806–810 (2014).
52. Vidal, J. P. *et al*. Multilevel and multiscale drought reanalysis over France with the Safran-Isba-Modcou hydrometeorological suite. *Hydrol. Earth Syst. Sci. Discuss.* **14**, 459–478 (2010).
53. Burnham, K. P. & Anderson, D. R. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (Springer Science & Business Media) (2003).
54. Zuur, A. F. *et al. Mixed effects models and extensions in ecology with R* 447–458 (Springer New York) (2009).
55. Bates, D., Maechler, M., Bolker, B., Walker, S. & others lme4: Linear mixed-effects models using Eigen and S4. *R Package Version* **1** (2014).

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Author Contributions

T.C. and S.D. conceived the idea for this work. T.C., C.F. and M.N. assembled the dataset and analyzed the data. T.C. and S.D. wrote the manuscript and A.K., S.V., M.N. and C.F. revised the manuscript.

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Fruiting Strategies of Perennial Plants: A Resource Budget Model to Couple Mast Seeding to Pollination Efficiency and Resource Allocation Strategies

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ABSTRACT: Masting, a breeding strategy common in perennial plants, is defined by seed production that is highly variable over years and synchronized at the population level. Resource budget models (RBMs) proposed that masting relies on two processes: (i) the depletion of plant reserves following high fruiting levels, which leads to marked temporal fluctuations in fruiting; and (ii) outcross pollination that synchronizes seed crops among neighboring trees. We revisited the RBM approach to examine the extent to which masting could be impacted by the degree of pollination efficiency, by taking into account various logistic relationships between pollination success and pollen availability. To link masting to other reproductive traits, we split the reserve depletion coefficient into three biological parameters related to resource allocation strategies for flowering and fruiting. While outcross pollination is considered to be the key mechanism that synchronizes fruiting in RBMs, our model counterintuitively showed that intense masting should arise under low-efficiency pollination. When pollination is very efficient, medium-level masting may occur, provided that the costs of female flowering (relative to pollen production) and of fruiting (maximum fruit set and fruit size) are both very high. Our work highlights the powerful framework of RBMs, which include explicit biological parameters, to link fruiting dynamics to various reproductive traits and to provide new insights into the reproductive strategies of perennial plants.

Keywords: masting, resource budget model, fruit set, fruit size, sex allocation, pollination efficiency.

Introduction

Masting—or mast seeding—is a reproductive strategy characterized by seed production that varies considerably from year to year yet is synchronized at the population level (Janzen 1976; Silvertown 1980; Kelly 1994). Masting has been reported in diverse perennial plants and is considered to evolve in various ecological contexts (Herrera et al. 1998; Kelly and Sork 2002; Koenig et al. 2003). Seeds produced by masting are a pulsed resource and, as such, are likely to greatly influence the demography and evolution of seed consumer populations and, in turn, the dynamics of the entire community (Ostfeld and Keesing 2000; Yang et al. 2010). One well-accepted selective advantage of masting is to lower the risk of seed predation: while most years of poor seed production keep consumer populations at a low level, uncommon, unpredictable mast years satiate consumers, thereby ensuring a large proportion of seeds escape from predation (Janzen 1971; Silvertown 1980; Kelly and Sork 2002). As another evolutionary issue of masting, the pollination efficiency hypothesis states that occasional high reproductive effort is concomitant with large pollen production, which increases pollination success (Smith et al. 1990; Kelly et al. 2001; Koenig and Ashley 2003; Pearse et al. 2014; Koenig et al. 2015).

While the evolutionary issue of masting and its impact on community dynamics are well documented, the proximate mechanisms governing masting are still much debated (Kelly and Sork 2002; Crone et al. 2009; Crone and Rapp 2014). A first set of hypotheses, reported in many studies, assumes that individual plants breed synchronously because they experience homogeneous climatic conditions and produce similar amounts of flowers and seeds in response (Inouye et al. 2002; Schauber et al. 2002; Kelly et al. 2013; see Kelly and Sork 2002 for a review). On the other hand, studies based on resource budget models (RBMs) propose an al-

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ternative to the explanation that masting is due to the effects of weather cues alone. Two factors are combined: (i) the intrinsic resource dynamics of the tree, that is, the way resources are allocated toward either storage or flowering and then fruiting; and (ii) the outcross pollination process that synchronizes fruiting among trees (see details below; Isagi et al. 1997; Satake and Iwasa 2000, 2002*a*; Crone and Rapp 2014).

RBMs make four statements: (i) Each year, an individual tree (or perennial plant) accumulates and stores energy or resources from photosynthesis or essential nutrient uptake from the soil. (ii) The tree does not reproduce unless it accumulates enough reserves. Once its reserves exceed a given threshold, the tree allocates all its excess reserves to flowers. (iii) Female flowers are fertilized by outcross pollen, with a success rate that is positively related to the amount of pollen produced by the neighboring trees (outcross pollination). (iv) Pollinated flowers then develop into mature fruits and incur resource depletion whose severity is governed by the resource depletion coefficient (DC), that is, the fruiting-to-flowering cost ratio (called k in Satake and Iwasa [2000], [2002*a*], [2002*b*] and R_c in Isagi et al. [1997]).

RBMs can produce some outputs similar to real masting data sets (Isagi et al. 1997; Satake and Iwasa 2000, 2002*a*, 2002*b*; Crone and Rapp 2014). In RBMs, fruiting fluctuates from one year to the next when the tree produces costly seed crops (with high DC values) that subsequently severely deplete resource reserves (Isagi et al. 1997). The outcross pollination, combined with pollen limitation, is considered to be one major force governing fruiting synchrony among trees. The few trees that may breed asynchronously and invest heavily into flowering while outcross pollen is rare are likely to have their flowers mostly unpollinated. Subsequent to fruiting failure, they may save resources, which may be invested in flowering the following year, possibly reaching synchrony with the other trees of the population (Satake and Iwasa 2000). Further theoretical investigations show that the synchrony level among trees is positively related to the spatial scale of pollen dispersal and may be strengthened by the Moran effect (i.e., environmental forcing; Rees et al. 2002; Satake and Iwasa 2002*b*).

Besides these investigations, we revisited RBMs to better understand how masting patterns articulate with other key reproductive characteristics of trees associated with pollination efficiency and resource allocation toward flowering and fruiting. In this perspective, we reconsidered the two key ingredients in RBMs, resource depletion and outcross pollination, which govern fruiting fluctuation at the tree level and fruiting synchrony among trees, respectively.

First, we modeled the outcross pollination process as a logistic function by determining, for a given individual tree, the probability for a female flower to develop into a mature fruit (fruit set) based on the amount of outcross pollen available. Previously, only power functions had been used to calculate this probability, even though such functions require the relationship between pollen availability and fruit set to be either strictly convex or strictly concave, depending on the power value (see fig. 1*A*). We hypothesized that a logistic relationship would better reflect reality because it would simultaneously capture both pollen dilution when pollen is sparse (associated with a convex increase in pollination success for power functions) and pollen saturation when pollen is abundant (a concave increase; see fig. 2*A*). In addition, pollination efficiency may also strongly impact tree resource dynamics and synchrony level and, hence, masting. Pollination efficiency may vary considerably depending on the mechanisms involved in gamete encounters (e.g., airborne vs. insect pollination; Regal 1982; Ackerman 2000) and on environmental features (such as tree density, landscape fragmentation, plant species assemblages in the community, or pollinator density; Allison 1990; Kunin 1997; Aguilar et al. 2006; Vamosi et al. 2006; Pellegrino et al. 2015). These mechanisms can be reflected through variable parameter values in a logistic function. Highly efficient pollination (fig. 2*A*, filled circles) is characterized by a quick, sharp increase in pollination success from very low amounts of outcross pollen in the environment. One notable example of this occurs for insect-pollinated plants when pollinators are abundant and readily and massively recruited as soon as the food resource (pollen) is detected (Rathcke 1983; Hegland 2014). By contrast, inefficient pollination creates strong inertia in the pollination success rate as long as small amounts of pollen are available (fig. 2*A*, open circles). Under limited pollen availability, a strong dilution effect means that very small amounts of pollen are trapped per female flower, thus leading to low fertilization success (Marshall and Folsom 1991; Wilcock and Neiland 2002; Aizen and Harder 2007; Eckert et al. 2010).

Second, we split the depletion coefficient into three biological components to explicitly link fruiting pattern to strategies of resource allocation for flowering and fruiting. The first component, hereafter called female flower allocation ratio (FA), is the proportion of the resources invested in flowering that is allocated to female flowers (vs. pollen) until fertilization. The second component, maximum fruit set (MFS), is the probability for a female flower to successfully develop into a mature fruit when pollen is not a limiting factor. The third component, fruiting-to-flowering resource demand ratio (FFR), is the ratio of the resources required to produce one mature fruit to that required for one sexually operational female flower. Considering a fixed amount of resources required to produce one flower within a tree population, FFR variation can be used as a proxy for mature fruit size variation. Trees may incur severe reserve depletion when they allocate most of their

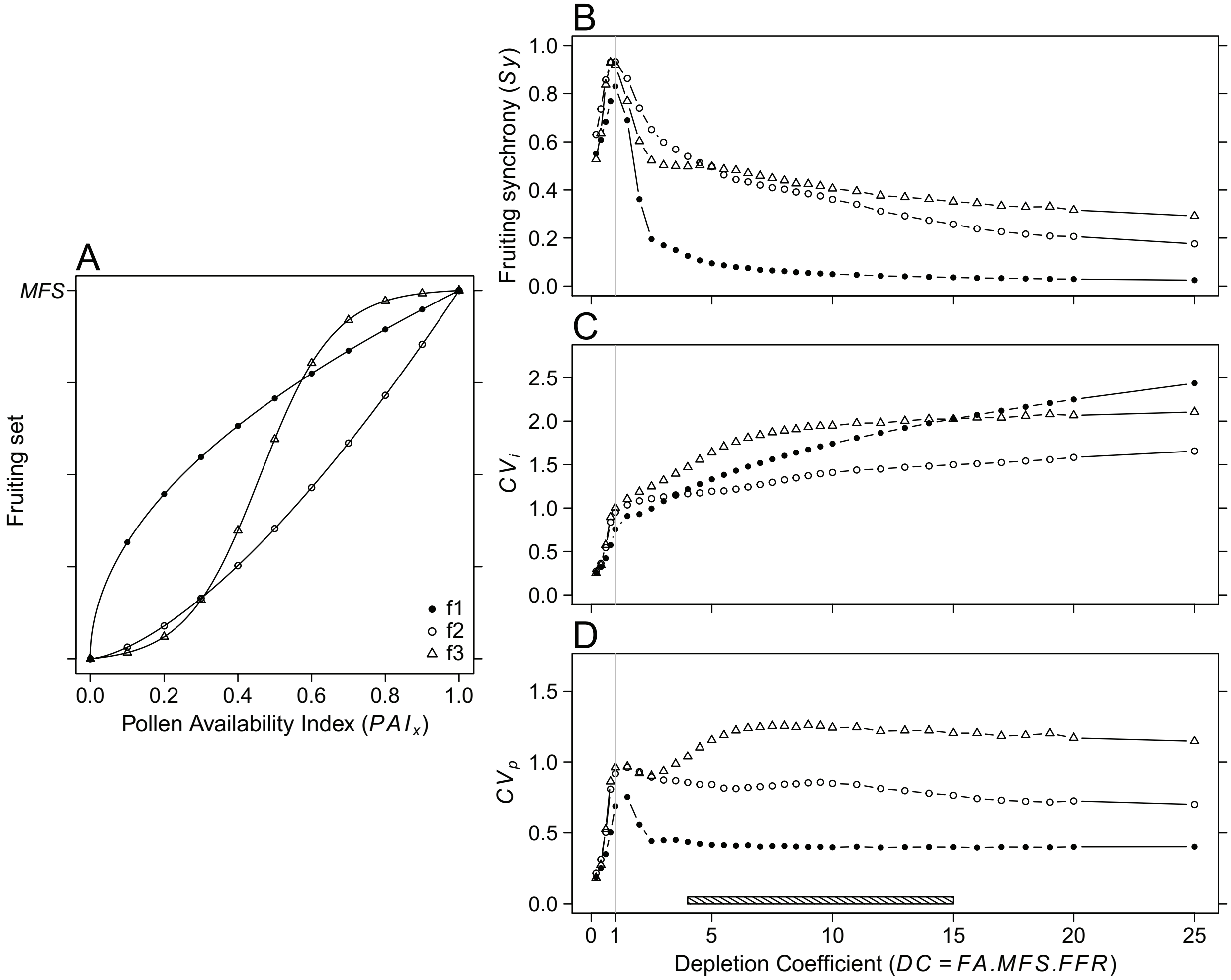

Figure 1: Fruiting dynamics as a function of the depletion coefficient (DC) and the shape of the outcross pollination function. *A*, The outcross pollination function determines the positive, nonlinear relationship between the amount of outcross pollen available in the neighborhood of tree x at year t ($\mathrm{PAI}_x(t)$) and the proportion of female flowers that were successfully pollinated ($P_x(t)$). Pollen availability index PAI_x ranges from 0 to 1 (from no pollen produced by all the neighboring trees to the maximum amount of pollen produced; see text). Three distinct outcross pollination functions were successively included in the model: two power functions already explored in previous models (function 1: $P_x(t) = (\mathrm{PAI}_x(t))^{1/2}$, function 2: $P_x(t) = (\mathrm{PAI}_x(t))^{3/2}$) and a logistic function bounded between 0 and 1 (function 3: $P_x(t) = 1/(1 + 100e^{-10.\mathrm{PAI}_x(t)})$; see eq. [3]). For each pollination function, the DC effect is shown on the fruiting synchrony among trees Sy (*B*) and on the fruiting variation across years at the individual tree level CV_i (*C*) and at the population level CV_p (*D*). The range of DC values empirically estimated for sessile oak trees is shown by the hatched horizontal bar above the *X*-axis.

flowering resource budget into female flowers or when they produce either a large fruit crop (i.e., associated with high pollination success and an elevated MFS value), large-sized fruits (a large FFR), or both.

To examine the relationship between fruiting dynamics and other key reproductive characteristics (e.g., outcross pollination process, resource allocation strategies for reproduction), we built a resource budget model that simulated fruiting dynamics of trees within a population (Isagi et al. 1997; Satake and Iwasa 2000, 2002*a*, 2002*b*). We examined fruiting dynamics through three distinct outputs: fruiting synchrony at the tree population level (Sy); the coefficient of variation in seed production across years at the individual tree level (CV_i), and the coefficient of variation in seed production across years at the tree population level (CV_p). Because a high CV_p value results from high fruiting synchrony among trees within a population combined with elevated temporal fruiting fluctuation at the tree level (Herrera 1998; Koenig et al. 2003), we considered that CV_p would accurately reflect masting intensity. In addition, to improve the realism of sensitivity analyses made on fruiting dynamics, we quantified MFS and the range of FFR values to be used with data from a field survey on sessile oak (*Quercus petraea*), oak trees being among the most

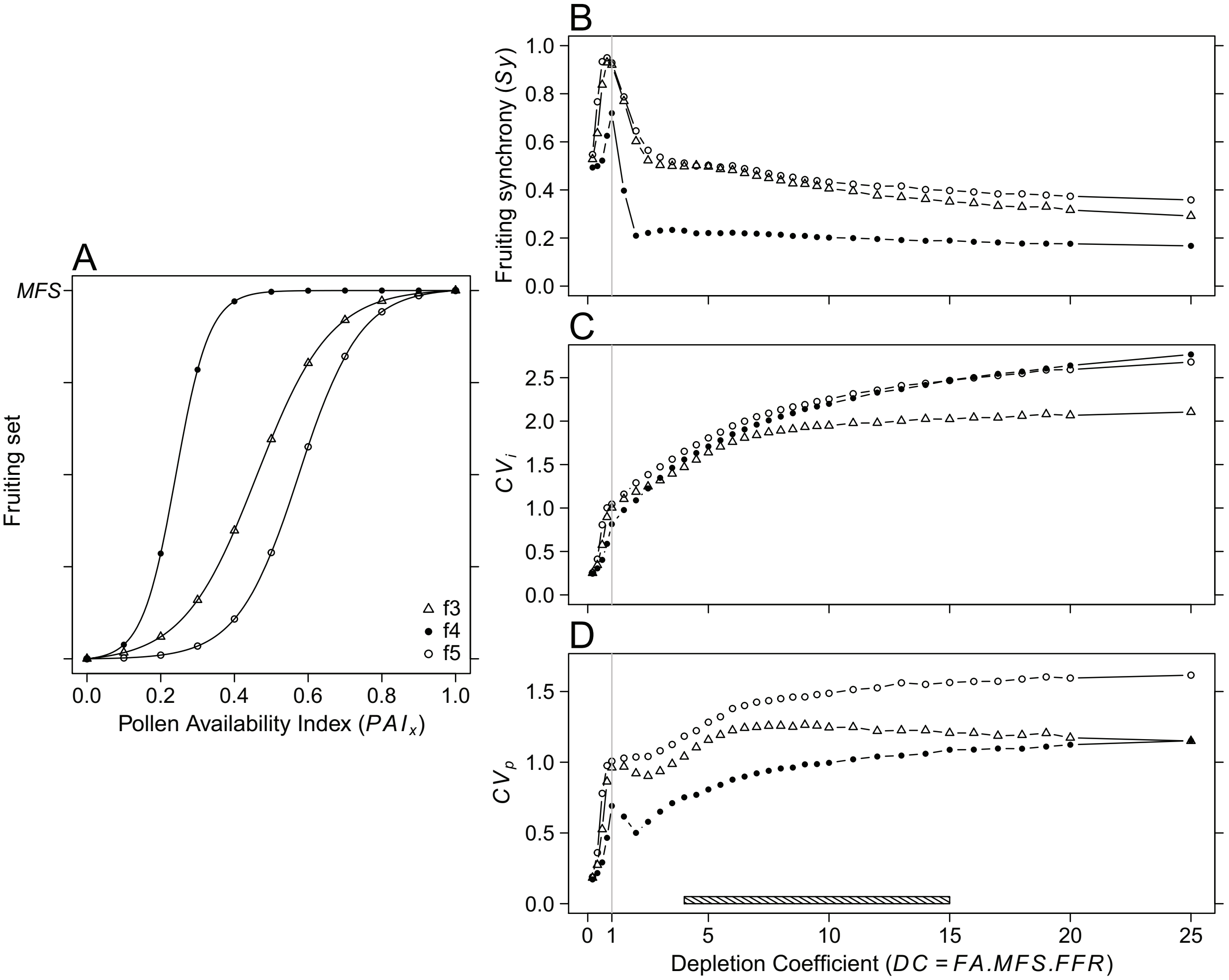

Figure 2: Impact of outcross pollination efficiency on fruiting dynamics. *A*, Three logistic-shaped pollination functions. Fruiting success increases in a logistic manner with pollen availability, according to three pollination efficiency levels, functions 3–5. Function 3: $P_x(t) = 1/(1 + 100e^{-10.\mathrm{PAI}_x(t)})$, function 4: $P_x(t) = 1/(1 + 200e^{-22.\mathrm{PAI}_x(t)})$, function 5: $P_x(t) = 1/(1 + 1{,}000e^{-12.\mathrm{PAI}_x(t)})$. *B–D*, See figure 1 legend.

emblematic mast-seeding species (Herrera et al. 1998; Kelly and Sork 2002; Koenig et al. 2003).

Material and Methods

We built a resource budget model accounting for tree resource dynamics and the outcross pollination process.

Modeling Tree Resource Dynamics

In our model, the forest was defined as being composed of a large number of trees of the same species, where each tree x occupied a distinct location on a two-dimensional grid. Accordingly, $S_x(t)$ was the level of resource reserves in tree x at the beginning of year t. Every year, each tree accumulated a fixed amount of resources from photosynthesis, Ps. Unless the level of resources $S_x(t)$ + Ps exceeded a threshold level L, the tree did not produce any flowers and stored the acquired resources until the following year. Whenever the level of resources exceeded L, tree x initiated reproduction by converting the amount of resources above L into flowering and allocating the proportion FA to female flowers, whose number was proportional to the excess reserve. Irrespective of pollen limitation, some flower abscission or fruit abortion is commonly observed in perennial plants (Stephenson 1981; Holland et al. 2004). Accordingly, we considered that, independently of any pollen limitation, only a proportion MFS of pollinated female flowers would successfully mature into fruit with the relative resource requirement FFR. The resources allocated toward fruiting then equal

$$\mathrm{FA} \cdot \mathrm{MFS} \cdot \mathrm{FFR} \cdot (S_x(t) + \mathrm{Ps} - L).$$

We assumed that fruiting might be followed by severe resource depletion, which would force the tree to replenish its reserves over several years before once again being able to flower. Overall, the absolute reserve of tree x at the onset of year $t+1$ can be computed as follows:

$$S_x(t+1) = \begin{cases} S_x(t) + \mathrm{Ps} - (1 + \mathrm{FA} \cdot \mathrm{MFS} \cdot \mathrm{FFR})(S_x(t) - L + \mathrm{Ps}) & \text{if } S_x(t) - L + \mathrm{Ps} > 0 \\ S_x(t) + \mathrm{Ps} & \text{if } S_x(t) - L + \mathrm{Ps} \leq 0 \end{cases} \tag{1}$$

(see Satake and Iwasa 2002*a* for details).

Equation (1) becomes nondimensionalized if $(S_x - L + \mathrm{Ps})/\mathrm{Ps}$ is replaced by Y_x, as follows:

$$Y_x(t+1) = \begin{cases} -\mathrm{FA} \cdot \mathrm{MFS} \cdot \mathrm{FFR} \cdot Y_x(t) + 1 & \text{if } Y_x(t) > 0 \\ Y_x(t) + 1 & \text{if } Y_x(t) \leq 0 \end{cases} \tag{2}$$

(Satake and Iwasa 2002*a*).

Here $Y_x(t+1)$ can be considered as the relative resource reserve of tree x at the onset of the year t once standardized per Ps unit, which is the fixed amount of resources gained yearly through photosynthesis.

We further enhanced this basic dynamic equation by accounting for outcross pollination and by introducing environmental stochasticity in the amount of resources acquired yearly by individual trees. As a result, equation (2) becomes

$$Y_x(t+1) = \begin{cases} -\mathrm{FA} \cdot \mathrm{MFS} \cdot \mathrm{FFR} \cdot P_x(t) Y_x(t) + 1 + \varepsilon_x(t) & \text{if } Y_x(t) > 0 \\ Y_x(t) + 1 + \varepsilon_x(t) & \text{if } Y_x(t) \leq 0 \end{cases}, \tag{3}$$

where $P_x(t)$ is the pollination success of tree x, and $\varepsilon_x(t)$ is the error that results from individual tree variability added to population-wide yearly variation (see below and Satake and Iwasa 2002*a*).

The Outcross Pollination Process

Because resource dynamics in themselves do not induce fruiting synchrony among trees, and because pollination efficiency overall depends on the availability of outcross pollen (Nilsson and Wastljung 1987; Smith et al. 1990), RBMs include an outcross pollination function that precludes self-pollination (Satake and Iwasa 2000). The number of fruits produced by a single tree in any given year, therefore, depends not only on the number of female flowers it produces but also on the amount of exogenous pollen available, which itself depends on the number of neighboring trees and on the amount of pollen they produce (see below). Fruiting also depends on an outcross pollination function that reflects the link between pollen availability and pollination success.

Determining the set of neighboring trees that might pollinate a focal tree. We developed a spatially explicit model in which trees were regularly distributed on a two-dimensional square grid defined as a tore to avoid edge effects. The distance between two trees located at (x_1, y_1) and (x_2, y_2), respectively, was calculated using the Moore neighborhood method. Any tree distant from focal tree x by less than a threshold value D could pollinate it; this situation occurred whenever $\max(|x_1 - x_2|, |y_1 - y_2|) \leq D$. At one extreme ($D = 1$), only the eight trees immediately adjacent to the focal tree on the grid could pollinate it, while at the other extreme, the whole forest could potentially contribute to pollinating the focal tree. How D impacts fruiting has been explored elsewhere (Satake and Iwasa 2002*a*): herein, we exclusively considered intermediate situations where only trees distant from the focal tree by less than 5 units on the grid (i.e., 120 neighboring trees) could pollinate it.

Determining the relative amount of outcross pollen available for a focal tree. As for female flowers, the amount of pollen produced any given year by any tree is proportional to the amount of its excess reserves at the onset of the reproductive season. For each tree, we calculated its relative pollen production, that is, the ratio of the amount of pollen it actually produced to the maximum amount it would have produced if all the reserves acquired through photosynthesis had been converted into flowers. For a given focal tree x, we then computed the pollen availability index (PAI, comprised between 0 and 1) as the summed relative pollen produced by its z neighboring trees:

$$\mathrm{PAI}_x(t) = \frac{1}{z} \sum_{y=1}^{z} \max(Y_y(t), 0). \tag{4}$$

The outcross pollen function. Following Satake and Iwasa (2000), we introduced the pollination success of tree x, $P_x(t)$, to account for outcross pollen limitations on reproduction. The pollination function P describes the strength of outcrossing pollination as a function of the amount of exogenous pollen available. This function has typically been defined as a positive power function. This means that at any year t, P_x continuously increases along with the total amount of exogenous pollen available in a concave, linear, or convex manner, depending on whether the positive coupling strength value β is below, equal to, or above 1, respectively (e.g., Satake and Iwasa 2002*a*, 2002*b*; Iwasa and Satake 2004). In our model, we compared the performance of two such positive power functions with several distinct logistic functions that seem to better fit the pollination process (see "Introduction"; figs. 1*A*, 2*A*).

Accounting for Environmental Stochasticity

There is empirical evidence that trees, even when they are distant from each other, reproduce synchronously partly because they experience similar environmental fluctuations (Koenig and Knops 1998, 2000, 2013). As did Satake and Iwasa (2002*b*), we introduced environmental noise $\varepsilon_x(t)$ into our model to account for the fact that the resources gained from photosynthesis by tree x may differ from one year to the next due to (i) climatic variations that evenly affect all the trees in the population and (ii) fine-scale environmental differences (e.g., soil characteristics, available nutrients, or water supply) affecting tree x only. Here $\varepsilon_x(t)$ accounts for individual stochastic variation in the resources accumulated by tree x at the onset of the reproductive season t; it can depart from the average population noise ε_{pop},which itself may vary from one year to the next, so that

$$\varepsilon_x \sim N(\varepsilon_{\text{pop}}, \sigma_{\text{env}}\sqrt{1-\text{Sy}_{\text{env}}}),$$

with

$$\varepsilon_{\text{pop}} \sim N(0, \sigma_{\text{env}}\sqrt{\text{Sy}_{\text{env}}}). \qquad (5)$$

Sy_{env} is the environmental synchrony among trees (the Moran effect) and is defined as the proportion of the total environmental variance (σ^2_{env}) that is due to population-scale variance. The Moran effect has been well studied elsewhere (see Satake and Iwasa 2002*b*), so in our model, we set intermediate, fixed values for σ^2_{env} and Sy_{env} (0.2 and 0.5, respectively). Environmental stochasticity, by affecting the resources gained by trees, indirectly impacts the amount of outcross pollen produced yearly. We then modified equation (4) to introduce stochasticity into the pollen availability index as

$$\text{PAI}_x(t) = \frac{1}{\sum_{y=1}^{z}[1+\varepsilon_y(t-1)]}\sum_{y=1}^{z}\max(Y_y(t), 0). \qquad (6)$$

Model Processing and Model Outputs: Sy, CV$_i$, and CV$_p$

In our model, we used a square grid comprising 400 trees. All simulations were run with a C++ algorithm. Each simulation lasted 2,000 time steps (years), but only the last 300 steps—independent from initial conditions—were used to compute parameters reflecting fruiting dynamics. We focused on three criteria classically used to describe masting: (i) the spatial synchrony of seed crop size among trees (Sy) and the temporal coefficient of variation in fruiting at the (ii) individual (CV_i) and (iii) population (CV_p) levels (Herrera 1998; Koenig et al. 2003). Here, Sy is the mean of all pairwise Pearson correlations between the time series for each pair of trees (Satake and Iwasa 2002*a*), CV_p is the coefficient of variation of the mean annual seed production computed for all 400 trees in the population, and CV_i describes individual tree between-year variability in seed production and is the mean of the coefficients of variation computed individually for the 400 trees (Herrera 1998; Koenig et al. 2003). We examined the extent to which fruiting dynamics (and, hence, masting) are sensitive to the outcross pollination function (two power and three distinct logistic functions tested; see figs. 1*A*, 2*A*) and to the depletion coefficient ($\text{DC} = \text{FA}\cdot\text{MFS}\cdot\text{FFR}$). We ran 100 simulations for each set of parameters, then computed and displayed the average Sy, CV_p, and CV_i.

Setting Up the Range of Values for the Depletion Coefficient in RBMs

We defined DC as the product of three biological components (FA, MFS, and FFR; see table 1). We estimated MFS and FFR based on data from a field survey of the flowering and fruiting effort of 130 sessile oak trees (*Quercus petraea*) from 13 populations distributed throughout metropolitan France (see app. A for detailed methods and results; apps. A, B available online). Assuming that oak trees invest resources equally into male and female flower production ($\text{FA} = 0.5$), we found DC mean values within populations ranging from 4 to 15. Similar results were obtained when considering either dry weight, carbon, or nitrogen as the limiting resource. This range of values is shown by hatched horizontal bars above the *X*-axis in figures 1*D* and 2*D*.

Based on this empirical evaluation, subsequent analyses were undertaken to assess the sensitivity of the RBM outputs to extended DC values (from 0 to 25), that match DC values potentially found in various perennial plant species. Because FFR estimates were found to be highly variable among trees from the same localities (CV_{FFR} averaging 0.4 per site in our field survey; see app. A), we further examined the impact of variations in individual DC values (CV_{DC} ranging from 0 to 1) on fruiting dynamics (fig. B1, available online).

Results

Fruiting Dynamics as a Function of the Depletion Coefficient

Values for Sy and CV_i (fig. 1*B*, 1*C*) show similar patterns of variation along with DC values, irrespective of the outcross pollination function included in the model (see figs. 1*A*, 2*A*).

As pointed out by Isagi et al. (1997), very low DC values (near 0) indicate that almost no additional resources are required to produce a mature fruit from a female flower and that no resource depletion takes place. At the onset of each year, trees always exhibit excess reserve (eq. [1]) and therefore regularly produce flowers and fruits: as a

Table 1: Glossary

Parameter	Definition	Reference
$\mathrm{CV_i}$	Temporal coefficient of variation of fruiting at the tree level	Figs. 1, 2
$\mathrm{CV_p}$	Temporal coefficient of variation of fruiting at the population level	Figs. 1, 2
DC	Depletion coefficient is the fruiting relative to flowering effort (also called k in Satake and Iwasa [2000], [2002*a*], [2002*b*] and R_c in Isagi et al. [1997]); here, it is computed as the product FA · MFS · FFR	. . .
FA	Female flower allocation ratio is the proportion of resources a tree may allocate to its female flowers prior to fertilization among the excess reserves allocated to flowering	Eqq. (1)–(3)
FFR	Fruiting-to-flowering resource-demanding ratio is the ratio of the additional resources required to produce a mature fruit from a female flower to that required to produce a female flower; by extent, FFR may be considered as a proxy for fruit size; in the model, it is considered constant for individual trees	Eq. (1)
L	Threshold level of resources above which flowering occurs	Eq. (1)
MFS	Maximum fruit set is the probability for a fertilized female flower to develop into a mature fruit; when multiplied with $P_x(t)$, it gives the fruiting success	Eqq. (1)–(3)
$\mathrm{PAI}_x(t)$	Pollen availability index computes the relative amount of outcross pollen available for tree x at year t; it depends on the amount of pollen produced by trees present in the neighborhood of tree x	Eqq. (4), (5)
Ps	Resources gained yearly from photosynthesis	Eq. (1)
$P_x(t)$	Pollination success of tree x at year t depends on PAI and on the outcross pollination function that is either a power or logistic one in this study; it is involved in the fruiting success, i.e., the probability for a female flower to develop into a mature fruit	Eq. (3); figs. 1*A*, 2*A*
$S_x(t)$	Absolute resource reserve of tree x at the onset of year t	Eq. (1)
Sy	Synchrony level in fruit crop size among trees	Figs. 1, 2
$Y_x(t)$	Resource reserve of tree x at the onset of year t standardized per Ps unit, i.e., the resources gained yearly through photosynthesis	Eqq. (1), (2)

consequence, they show low $\mathrm{CV_i}$ values (fig. 1*C*). The rather elevated fruiting synchrony observed simultaneously in the population (around 0.5) mainly results from moderate environmental forcing ($\mathrm{Sy_{env}}$; see eq. [5]), with only weak fruiting variation between years (low $\mathrm{CV_i}$ and $\mathrm{CV_p}$; fig. 1*C*, 1*D*).

When DC increases to 1, fruiting synchrony and $\mathrm{CV_i}$ both increase. When the fruiting cost equals that of flowering ($\mathrm{DC} = 1$), fruiting dynamics follow a very regular 2-year pattern, with 1 year of high fruiting alternating with 1 year of low (or almost no) fruiting. Such extremely regular fluctuations at the tree level promote maximum synchrony among trees (fig. 1*B*) due to the outcross pollination process, as has already been shown in detail in previous work (Isagi et al. 1997; Satake and Iwasa 2000).

For DC values above 1, $\mathrm{CV_i}$ goes on increasing monotonically—though at a lower rate (fig. 1*C*)—while Sy rapidly declines (fig. 1*B*). Such DC values are accompanied by chaotic fruiting dynamics at the tree level, thus reducing the opportunity for fruiting synchronization within the population (as shown by decreasing Sy). For higher DC values (above 5), fruiting synchrony decreases asymptotically down to relatively stable values. The asymptotic-like synchrony level (considering strong fluctuations at the individual tree level, i.e., high $\mathrm{CV_i}$; fig. 1*C*) is closely related to the outcross pollination function, higher synchronization being predicted with logistic rather than power functions.

Here $\mathrm{CV_p}$, resulting from the combined effects of $\mathrm{CV_i}$ and Sy and being positively correlated to these two parameters, shows a more complex relationship with DC (fig. 1*D*): $\mathrm{CV_p}$ first rapidly increases as DC increases up to 1 due to a concomitant increase in Sy and $\mathrm{CV_i}$ and then sharply and briefly declines, owing to the marked decrease in Sy, while $\mathrm{CV_i}$ continues to increase slightly. For higher DC values, $\mathrm{CV_p}$ values differ according to the outcross pollination function used.

Fruiting Dynamics and the Shape of Outcross Pollination Function

The outcross pollination process has formerly been modeled as a power function with β, the power of the function. With $\mathrm{DC} > 3$ and small β values, no masting was found (fig. 1*A*, 1*D*, filled circles; function 1 [f1], $\beta = 1/2$, $\mathrm{CV_p}$, is around 0.4). For high β values, moderate masting was observed (fig. 1*A*, 1*D*, open circles; f2, $\beta = 3/2$, $\mathrm{CV_p}$, is between 0.8 and 1 for $1 < \mathrm{DC} < 5$ and then stays below 0.8 for $\mathrm{DC} > 5$). Neither power function was able to predict the highest $\mathrm{CV_p}$ values, either due to loose tree synchrony (for low β values; fig. 1*B*) or to low $\mathrm{CV_i}$'s (for large β values; fig. 1*C*). Values for $\mathrm{CV_p}$ were the highest for the logistic-shape outcross pollination function (around 1 or above) and remained high over a large range of DC values (from $DC > 5$; fig. 1*D*).

Fruiting Dynamics and Pollination Efficiency

Values for CV_p, resulting from CV_i and Sy, may reach their highest through two distinct pathways depending on the efficiency of the pollination process modeled from various logistic functions (fig. 2*A*). Outcross pollination appears to be the key mechanism that synchronizes fruiting, as shown in previous studies with RBMs. However, our model predicts that masting should be most intense, even over a large range of DC values, only when pollination efficiency is weak (fig. 2*A*, 2*D*, open circles: CV_p around 1.5). The logistic function associated with less efficient pollination shows strong inertia in the pollination success and consequently favors homogeneous pollination success among the trees, as long as pollen availability remains low (e.g., for a pollen availability index between 0 and 0.3; fig. 2*A*). Such logistic pollination function thus should promote high fruiting synchrony among trees (Sy; fig. 2*B*) together with marked fluctuations in fruiting at the tree level (CV_i) which, taken together, explain the very high CV_p values obtained (fig. 2*C*, 2*D*).

On the contrary, when pollination is very efficient, the fruiting success of a tree may increase sharply from very small amounts of pollen available. Even if neighboring trees experience subtle differences in the amount of outcross pollen received, they may experience markedly distinct pollination success and, hence, may be easily desynchronized in their seed production (fig. 2*B*, filled circles: low Sy values). Despite weak synchrony, moderate masting may still occur, provided that very high DC values are reached (fig. 2*C*, 2*D*; CV_p reaching 1 for $DC > 15$).

Moderately efficient pollination should be accompanied by intense masting starting at rather low DC values, with trees remaining synchronized (fig. 2*B*, 2*D*; $DC > 5$, CV_p around 1.2). Yet, this situation also generates the lowest CV_i values (fig. 2*C*, open triangles).

Fruiting Dynamics When DC Fluctuates among Trees

Fruiting dynamics were only weakly affected by variations in the DC heterogeneity level among trees within a population (for CV_{DC} less than 0.4; see app. B; fig. B1). When DC becomes more variable among trees, Sy and CV_i both subtly decline, resulting in slightly declining CV_p (from 1 down to 0.8 for CV_{DC} varying from 0.4 to 1; see fig. B1).

Discussion

In this study, we revisited the way RBMs could generate masting by using logistic functions linking pollination success to pollen availability to model the outcross pollination process. In addition, we split the depletion coefficient into three explicit biological parameters that reflect how trees allocate their resources to flowering and fruiting (i.e., FA, MFS, FFR; see table 1). Our results show that masting is much more often observed when the outcross pollination process is modeled using logistic functions than with the power functions used until now (Isagi et al. 1997; Satake and Iwasa 2000, 2002*a*, 2002*b*). While outcross pollination is the key process shown to synchronize fruiting in RBMs, our results point out that masting would be most intense when pollination is ineffective. Masting should nevertheless occur when pollination is very efficient yet be restricted to high depletion coefficient values: this can be the case whenever plants massively allocate their flowering effort into female items (i.e., high FA), reach high maximum fruit set under nonlimiting pollen availability (high MFS), and/or mature large-sized fruits compared to female flower size (high FFR).

Previous studies used power-like functions to link pollination success with the amount of outcross pollen available; they examined the fruiting dynamic using a rather narrow range of low depletion coefficient values ($DC < 5$) and analyzed masting based on fruiting synchrony among trees (equivalent to Sy in this study; figs. 1*B*, 2*B*; Isagi et al. 1997; Satake and Iwasa 2000, 2002*a*, 2002*b*). According to these studies, opportunities for masting emergence are expected to sharply decrease as the depletion coefficient increases. Here, we estimated DC in several sessile oak populations and found them to vary from 4 to 15 on average, depending on the population studied (see app. A). This range should probably be extended even when considering other oak species or perennial plants that may produce bigger, costlier fruits. When the depletion coefficient value was realistically high ($DC > 5$), our model showed that the two power-like pollination functions failed to predict intense masting ($CV_p \lesssim 0.8$). Values for CV_p remained low due to either low fruiting synchrony levels (for low β value; fig. 1*A*, 1*B*, filled circles) or low individual fruiting fluctuation (for high β value; fig. 1*A*, 1*C*, open circles).

By contrast, our model showed that masting occurred frequently and was most intense (high CV_p), even with elevated DC values (>5), when a logistic relationship between pollen availability and pollination success was accounted for (figs. 1, 2). Our model was further able to disentangle contrasted ways leading to masting, depending on pollination process efficiency. While outcross pollination is central to fruiting synchrony in RBMs, our results counterintuitively showed that masting may be most intense (as shown by consistently high CV_p values along the DC gradient) when pollination is nearly ineffective (fig. 2*D*). At low or medium pollen availability, the slow increase in the pollination success (fig. 2*A*, f5, open circles) would ensure weak but homogeneous pollination among neighboring trees, leading to their close fruiting synchronization. Inefficient pollination maximizes masting also because it is associated with high CV_i values ($CV_p \leq 1.5$ for $DC > 10$). On the contrary, very efficient pollination is characterized by a rapid increase in pollination success as soon as low amounts of pollen are available (fig. 2*A*, f4, filled circles). This process causes trees to get desynchronized because pollen is a less limiting factor: the fruiting dynamics of each tree more closely depend on its own reserve levels than on local exogenous pollen production. However, when pollination is highly effective, medium-level masting may still occur, provided that the depletion coefficient is very high: despite poor tree synchrony, strong fruiting fluctuation is expected at the tree level (high CV_i), which results in intermediate fruiting fluctuation at the population level ($CV_p \approx 1$ for $DC \approx 25$; fig. 2*D*). When pollination is moderately efficient (fig. 2*A*, f3, open triangles), masting intensity should be moderate and stable over a large DC gradient (fig. 2*D*).

The unexpected finding of intense masting under inefficient pollination could be tested in several different ways. First, comparisons could be made between plant species with markedly distinct pollination mechanisms. For example, pollination should be more efficient—and masting, therefore, less intense—under low pollen density in insect-pollinated species than in wind-pollinated species. Insect pollinators, at least when their populations are dense, may be actively and even exponentially recruited as soon as a small amounts of food (pollen) are detected (Rathcke 1983; Hegland 2014). In agreement with this prediction, insect-pollinated species seem to exhibit overall less intense masting than do wind-pollinated species (Kelly and Sork 2002). Among wind-pollinated species, higher pollination efficiency and less intense masting would also be expected in species that have evolved organs to accumulate pollen close to stigmata (e.g., conifer ovulate cones [Niklas 1982]) than in those whose stigmata are passively exposed to aerial pollen. Second, comparisons could be made within a given plant species between populations undergoing various degrees of pollination efficiency owing to distinct environmental constraints. Our model indirectly predicts that intense masting would occur under low plant densities or in highly fragmented populations, since in both situations, pollination should be less efficient for a given mean plant flowering effort. Among insect-pollinated species, intense masting is expected either when density/diversity in pollinators is low or when many plant species severely compete for the same insect pollinators (Allison 1990; Kunin 1997; Aguilar et al. 2006; Vamosi et al. 2006; Pellegrino et al. 2015).

Resource budget models are not only robust predictors of masting, they may also provide an integrative theoretical framework for jointly analyzing mechanisms in perennial plants related to reproductive strategies such as sex allocation strategies (linked to female flower allocation ratio, FA), fruit set and the trade-off between fruit number and fruit size (linked to maximum fruit set, MFS, and fruiting-to-flowering ratio, FFR), outcross pollination efficiency, and fruiting dynamics over time and space (described from Sy, CV_i, and CV_p). Introducing explicit biological parameters into RBMs also offers the opportunity to provide realistic scenarios for possible changes in plant fruiting patterns under climate change by examining the sensitivity of RBM parameters to climate variables. RBMs with explicit biological parameters, therefore, open new paths and testable predictions to explore the diversified mechanisms operating on the fruiting processes of perennial plants, their complex interactions, and, by extension, the proximate and ultimate causes of fruiting strategies.

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Literature Cited

Ackerman, J. D. 2000. Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. Plant Systematics and Evolution 222:167–185.

Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology Letters 9:968–980.

Aizen, M. A., and L. D. Harder. 2007. Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. Ecology 88:271–281.

Allison, T. D. 1990. Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. Ecology 71:516–522.

Crone, E. E., E. Miller, and A. Sala. 2009. How do plants know when other plants are flowering? resource depletion, pollen limitation and mast-seeding in a perennial wildflower. Ecology Letters 12: 1119–1126.

Crone, E. E., and J. M. Rapp. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. Annals of the New York Academy of Sciences 1322:21–34.

Eckert, C. G., S. Kalisz, M. A. Geber, R. Sargent, E. Elle, P. O. Cheptou, C. Goodwillie, et al. 2010. Plant mating systems in a changing world. Trends in Ecology and Evolution 25:35–43.

Hegland, S. J. 2014. Floral neighbourhood effects on pollination success in red clover are scale-dependent. Functional Ecology 28:561–568.

Herrera, C. 1998. Population-level estimates of interannual variability in seed production: what do they actually tell us? Oikos 82:612–616.

Herrera, C., P. Jordano, and J. Guitián. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. American Naturalist 152:576–594.

Holland, J. N., J. L. Bronstein, and D. L. DeAngelis. 2004. Testing hypotheses for excess flower production and low fruit-to-flower ratios in a pollinating seed-consuming mutualism. Oikos 3:633–641.

Inouye, D. W., M. A. Morales, and G. J. Dodge. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. Oecologia (Berlin) 130:543–550.

Isagi, Y., K. Sugimura, A. Sumida, and H. Ito. 1997. How does masting happen and synchronize? Journal of Theoretical Biology 187:231–239.

Iwasa, Y., and A. Satake. 2004. Mechanisms inducing spatially extended synchrony in mast seeding: the role of pollen coupling and environmental fluctuation. Ecological Research 19:13–20.

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465–492.

———. 1976. Why bamboos wait so long to flower. Annual Review of Ecology and Systematics 7:347–391.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution 9:465–470.

Kelly, D., A. Geldenhuis, A. James, E. P. Holland, M. J. Plank, R. E. Brockie, P. E. Cowan, et al. 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. Ecology Letters 16:90–98.

Kelly, D., D. E. Hart, and R. B. Allen. 2001. Evaluating the wind pollination benefits of mast seeding. Ecology 82:117–126.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? Annual Review of Ecology and Systematics 33:427–447.

Koenig, W. D., and M. V Ashley. 2003. Is pollen limited? the answer is blowin' in the wind. Trends in Ecology and Evolution 18:157–159.

Koenig, W. D., D. Kelly, V. L. Sork, R. P. Duncan, J. S. Elkinton, M. S. Peltonen, and R. D. Westfall. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. Oikos 102:581–591.

Koenig, W. D., and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. Nature 396:225–226.

———. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. American Naturalist 155:59–69.

———. 2013. Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. Ecology 94:83–93.

Koenig, W. D., J. M. H. Knops, W. J. Carmen, and I. S. Pearse. 2015. What drives masting? the phenological synchrony hypothesis. Ecology 96:184–192.

Kunin, W. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology 85:225–234.

Marshall, D. L., and M. W. Folsom. 1991. Mate choice in plants: an anatomical to population perspective. Annual Review of Ecology and Systematics 22:37–63.

Niklas, K. J. 1982. Simulated and empiric wind pollination patterns of conifer ovulate cones. Proceedings of the National Academy of Sciences of the USA 79:510–514.

Nilsson, S. G., and U. Wastljung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. Ecology 68:260–265.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15:232–237.

Pearse, I. S., W. D. Koenig, K. A. Funk, and M. B. Pesendorfer. 2014. Pollen limitation and flower abortion in a wind-pollinated, masting tree. Bulletin of the Ecological Society of America 95:462–464.

Pellegrino, G., F. Bellusci, and A. M. Palermo. 2015. Effects of population structure on pollen flow, clonality rates and reproductive success in fragmented *Serapias lingua* populations. BMC Plant Biology 15:222.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pages 305–329 *in* L. Real, ed. Pollination biology. Academic Press, New York.

Rees, M., D. Kelly, and O. N. Bjørnstad. 2002. Snow tussocks, chaos, and the evolution of mast seeding. American Naturalist 160:44–59.

Regal, P. J. 1982. Pollination by wind and animals: ecology of geographic patterns. Annual Review of Ecology and Systematics 13: 497–524.

Satake, A., and Y. Iwasa. 2000. Pollen coupling of forest trees: forming synchronized and periodic reproduction out of chaos. Journal of Theoretical Biology 203:63–84.

———. 2002*a*. Spatially limited pollen exchange and a long-range synchronization of trees. Ecology 83:993–1005.

———. 2002*b*. The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. Journal of Ecology 90:830–838.

Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. Ecology 83:1214–1225.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society 14:235–250.

Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1990. The advantage of mast years for wind pollination. American Naturalist 136:154–166.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics 12:253–279.

Vamosi, J. C., T. M. Knight, J. A. Steets, S. J. Mazer, M. Burd, and T.-L. Ashman. 2006. Pollination decays in biodiversity hotspots. Proceedings of the National Academy of Sciences of the USA 103:956–961.

Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. Trends in Plant Science 7:270–277.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.

References Cited Only in the Online Appendixes

Arceo-Gomez, G., and T.-L. Ashman. 2014. Patterns of pollen quantity and quality limitation of pre-zygotic reproduction in *Mimulus guttatus* vary with co-flowering diversity. Oikos 123:1261–1269.

Ashman, T. L., T. M. Knight, and J. A. Steets. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology 85:2408–2421.

Stone, J. L., J. D. Thomson, and S. J. Dent-Acosta. 1995. Assessment of pollen viability in hand-pollination experiments: a review. American Journal of Botany 82:1186–1197.

Venner, S., A. Siberchicot, P.-F. Pélisson, E. Schermer, M-C. Bel-Venner, M. Nicolas, F. Débias, et al. 2016. Data from: Fruiting strategies of perennial plants: a resource-budget model to couple mast seeding to pollination efficiency and resource allocation strategies. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.77kj5.

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POPULATION ECOLOGY – ORIGINAL RESEARCH

Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar

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Abstract Pulsed resources influence the demography and evolution of consumer populations and, by cascading effect, the dynamics of the entire community. Mast seeding provides a case study for exploring the evolution of life history traits of consumers in fluctuating environments. Wild boar (*Sus scrofa*) population dynamics is related to seed availability (acorns/beechnuts). From a long-term monitoring of two populations subjected to markedly different environmental contexts (i.e., both low vs. high frequency of pulsed resources and low vs. high hunting pressure in Italy and in France, respectively), we assessed how pulsed resources shape the reproductive output of females. Using path analyses, we showed that in both populations, abundant seed availability increases body mass and both the absolute and the relative (to body mass) allocation to reproduction through higher fertility. In the Italian population, females equally relied on past and current resources for reproduction and ranked at an intermediate position along the capital-income continuum of breeding tactics. In contrast, in the French population, females relied on current more than past resources and ranked closer to the income end of the continuum. In the French population, one-year old females born in acorn-mast years were heavier and had larger litter size than females born in beechnut-mast years. In addition to the quantity, the type of resources (acorns/beechnuts) has to be accounted for to assess reliably how females allocate resources to reproduction. Our findings highlight a high plasticity in breeding tactics in wild boar females and provide new insight on allocation strategies in fluctuating environments.

Keywords Body mass · Breeding tactics · Fluctuating environments · Masting · Path analysis

Introduction

Many terrestrial and aquatic ecosystems are characterized by pulsed resources (Ostfeld and Keesing 2000; Yang et al. 2008) that display a huge variation in their availability (Ostfeld and Keesing 2000). Mast seeding, which corresponds to intermittent production of large seed crops at the tree population level, provides a well-known example of pulsed resources in terrestrial ecosystems (Ostfeld and Keesing 2000). Intermittent production of abundant resources is likely to influence both population (e.g., Schmidt 2003) and community (Ostfeld and Keesing 2000; Holt 2008) dynamics of consumers. Such events should also affect life history and behavioral tactics at the individual level (Yang

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et al. 2008). For instance, mobile specialist consumers can move from one area to another one to track patchy pulsed resources like reported in the extinct Passenger Pigeon (*Ectopistes migratorius*) that tracks acorn-mast events across distinct localities (Blockstein and Tordoff 1985). Opportunistic resident consumers can switch their diet in response to pulsed resources as illustrated by black bears (*Ursus americanus*) that consume a higher proportion of acorns in mast years than in non-mast years (McDonald and Fuller 2005).

A pioneering review has hypothesized that pulsed-resource consumers may also respond to mast seeding via a change in reproductive output (Ostfeld and Keesing 2000). In particular, poorly mobile species and also species with a high capacity to increase their reproductive output (e.g., high average litter size) are expected to increase their reproductive output in response to mast seeding. Interestingly, a recent meta-analysis has shown that these expected relationships actually hold for mammals by considering species average body mass as a proxy of mobility and species average litter size as a measure of capacity to increase reproductive output (Bogdziewicz et al. 2016). Ten years ago, a landmark case study of reproduction in two species of squirrels (*Tamiasciurus hudsonicus* and *Sciurus vulgaris*) that consume variable seed resources has shown that the squirrel reproductive output increases before a mast seeding event, leading to increase population size in synchrony with resource pulses (Boutin et al. 2006). Therefore, both theoretical and empirical evidence for a change in reproductive output as a response to mast seeding has recently flourished in the literature. However, how the reproductive output is shaped by variation in pulsed resources within a species subjected to markedly different environmental contexts of seed availability remains an open question. We fill this knowledge gap here by assessing how pulsed resources shape the individual reproductive output of wild boar (*Sus scrofa*) females and its temporal variation in two populations strongly different in terms of ecological conditions.

Wild boar are opportunistic resident consumers, and are one of the most widely distributed mammals in the world (Massei and Genov 2004). They display an omnivore diet, but when available, acorns (i.e., oak mast) and beechnuts (i.e., beech mast) are highly preferred to any other food resources (Abrams 1990; Massei et al. 1996; Servanty et al. 2009). By feeding on forest mast, wild boar face with highly changing and unpredictable pulsed food resources (Gamelon et al. 2013) and strongly respond to these fluctuating resources. The growth rate of wild boar populations is closely related to the presence or absence of deciduous trees such as oak and beech (Jedrzejewska et al. 1997; Bieber and Ruf 2005), and the intensity of both past and current mast influences the timing of oestrus and the proportion of breeding females in a given year (Servanty et al. 2009).

We took advantage of a unique long-term monitoring of two wild boar populations to investigate how pulsed resources shape the allocation to reproduction by females in markedly different ecological contexts. Pulsed resources were fluctuating in both study areas. However, the two sites differed in terms of climate, tree composition and therefore in patterns of seed production. The two sites also strongly differed in terms of hunting pressure. While in the Italian site, wild boar faced with a low frequency of years with abundant seed production and a low hunting pressure (Focardi et al. 2008), the French site was characterized by a high frequency of years with abundant seed availability and a high hunting pressure (Servanty et al. 2009, 2011). In both populations, detailed information on yearly fruit production and female reproductive traits was available, allowing us to investigate the effects of past and current seed production on litter size. To account for the well-established positive effect of body mass on female fertility and litter size in terrestrial large mammals (Albon et al. 1986; Gaillard et al. 1992; Gerhart et al. 1997; Hewison and Gaillard 2001), we assessed the effects of seed availability on reproductive traits through possible nested effects of female body mass. Therefore, using path analyses (Shipley 2009, 2013), we tested whether intense past and/or current seed production influenced reproductive traits (1) only indirectly through female body mass, (2) directly without operating through female body mass, or (3) both directly and indirectly through female body mass.

Materials and methods

Study areas and populations

The study took place in two areas subjected to markedly different environmental contexts. One area was the 6000 ha fenced preserve at Castelporziano (41°44′N, 12°24′E) located near Rome (Italy). The climate in this area is Mediterranean, with dry summers and rainfall occurring mainly in October–November. The plant communities mainly consist of holly oak (*Quercus ilex*, 27%) and deciduous oak forests (*Quercus cerris* and *Quercus frainetto*, 34%), often associated with undergrowth of *Carpinus orientalis* (80–90%, Focardi et al. 2008; Servanty et al. 2011). The common oak (*Quercus robur*) is restricted to wet areas within the study site. Seed availability (i.e., acorns) was low for this wild boar population (Servanty et al. 2011). Moreover, as severe droughts occurred (Focardi et al. 2008), negative effects of water stress on seed availability cannot be excluded (see Koenig et al. 2013, p. 185–186). To count wild boar, artificial feeding mainly took place between

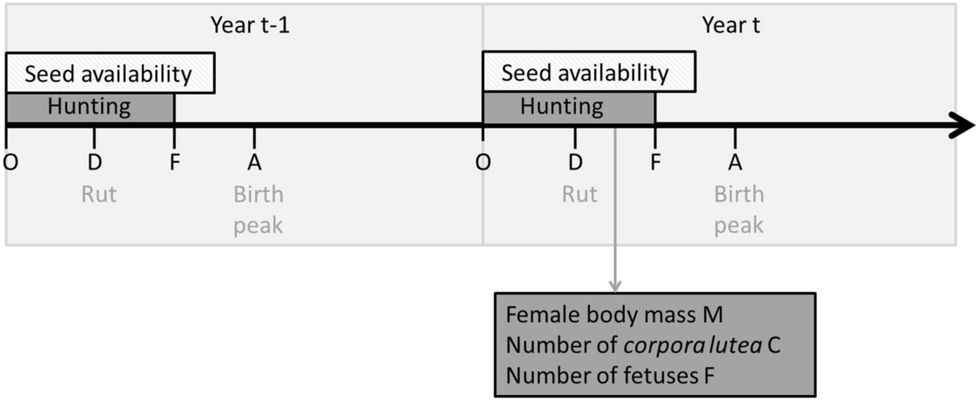


Fig. 1 Life cycle of the wild boar (*Sus scrofa*) with the hunting period, seed availability period, and type of data collected during the hunting season for two consecutive years. The capital letters *O*, *D*, *F*, *A* correspond to October, December, February and April months

end of June and late August (see Supplementary material Appendix 1, Table A1, for additional information on supplemental feeding in this study area). In addition, wild boar were only weakly hunted in autumn–winter (Fig. 1) to control the size of this enclosed population (Franzetti et al. 2012), the removal rates fluctuating between 0.08 and 0.15 over the studied period (see Supplementary material Appendix 1, Table A1). The population size was estimated to vary between 1700 and 2900 throughout the study period (see Supplementary material Appendix 1, Table A1). The annual survival of adult females was 0.706 [0.622; 0.790] (Focardi et al. 2008).

The other study site was the 11,000 ha forest at Châteauvillain-Arc-en-Barrois (48°02′N, 4°55′E) located in North-Eastern France. The climate in this area is intermediate between continental and oceanic types. The forest is mainly composed of oak (*Quercus petraea*, 41%) and beech (*Fagus sylvatica*, 30%). Pulsed resources such as acorns or beechnuts are frequent (Servanty et al. 2011) for this wild boar population whose population size was estimated to be between 1200 and 1500 individuals over the course of the study (Gamelon et al. 2011). In addition, each year between October and February, wild boar were harvested (see Supplementary material Appendix 2, Fig. A1) and the hunting pressure (measured as the ratio between the number of hunted marked individuals and the total number of marked individuals in the population) (Servanty et al. 2009) was high. The yearly probability for a wild boar to be killed by hunters was about 0.40 and reached 0.70 for adult males (Toïgo et al. 2008; Gamelon et al. 2011). The annual survival of adult females was 0.475 [0.437; 0.512] (Toïgo et al. 2008).

Wild boar data

While wild boar at Châteauvillain-Arc-en-Barrois are classified as *Sus scrofa scrofa*, wild boar at Castelporziano correspond to the Italian wild boar type *Sus scrofa majori* characterized by the absence of interbreeding with wild boar or domestic pig within the last century. Wild boar rut generally begins in mid-December but can occur a bit earlier in some years (Matschke 1964). Therefore, females are often pregnant when shot during the hunting season (Fig. 1). We only included pregnant females in this work. Live body mass at Castelporziano and dressed body mass (i.e., body mass without digestive tract, heart, lungs, liver, reproductive tract and blood) at Châteauvillain-Arc-en-Barrois have been recorded. At Châteauvillain-Arc-en-Barrois, information on both live and dressed body mass was available for 782 individuals between 2005 and 2015. As expected, a close relationship occurred between live and dressed body mass (live body mass = 1.907 + 1.225 * dressed body mass, $R^2 = 0.99$, unpublished data). We also recorded the age class of each pregnant female based on tooth eruption patterns (Matschke 1967). We distinguished juveniles (<1 year of age) from adults (>1 year of age). To measure fertility, we examined sagitally cut ovaries for the presence of *corpora lutea*. The presence of one or more *corpora lutea* for a female indicates that conception had occurred. In addition, the number of fetuses present in the uteri was recorded to evaluate litter size. It reflects how many fertilized blastocysts implanted and survived from potential mortality through resorption (Hewison and Gaillard 2001). Thus, an equal number of *corpora lutea* and fetuses reflects that the potential litter size equals the realized litter size and that no loss (hereafter embryonic mortality) occurred (see Supplementary material Appendix 3, Fig. A2, dotted lines). On the contrary, a higher number of *corpora lutea* than fetuses indicates that the potential litter size is larger than the realized litter size and that embryonic mortality occurred (see Supplementary material Appendix 3, Fig. A2, below dotted lines). Thus, the strength of the relationship linking the number of *corpora lutea* and fetuses reliably

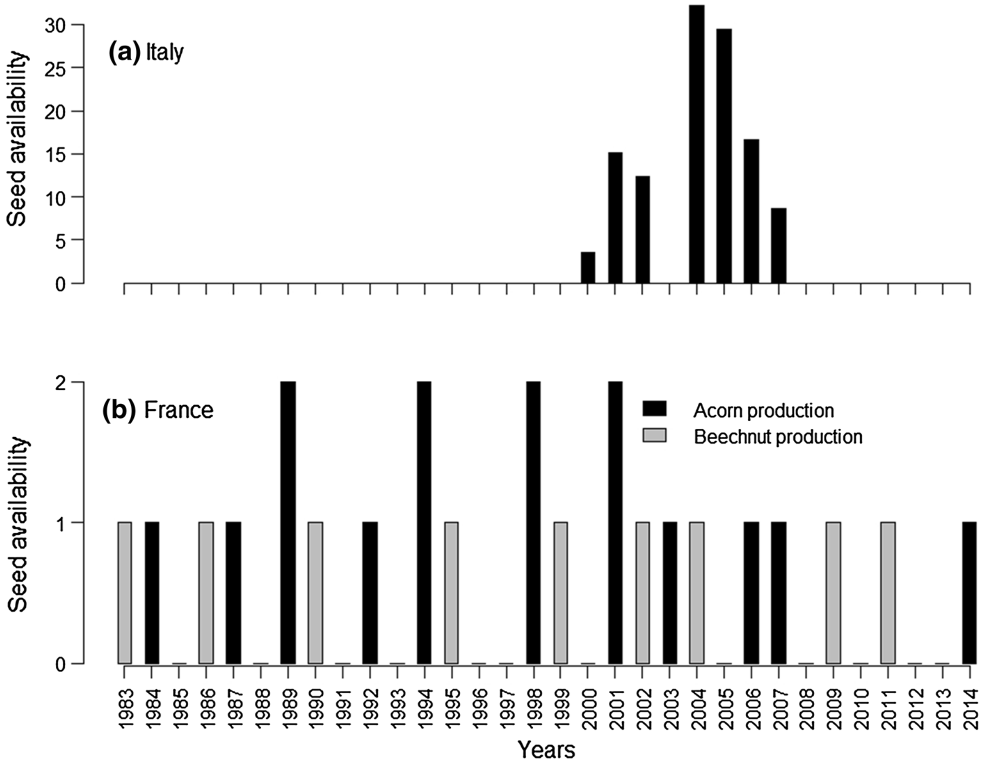


Fig. 2 For each hunting season, **a** the intensity of acorn production in Castelporziano, Italy, measured as the mean number of acorns per trap per year, and **b** the category of seed in Châteauvillain-Arc-en-Barrois, France, are reported. For this latter, four categories were considered: no mast production *N*, acorn years (split into acorn-mast years *A* and years of medium acorn production *AA*) and beechnut-mast years *B*

measures the amount of embryonic mortality. However, because females were shot at different gestation stages, this measure of embryonic mortality makes sense only if the fetus loss did not depend on the duration of pregnancy. It was actually the case for the two datasets we analyzed, for which an increase in the gestation stage had no detectable effect on the number of fetuses (Supplementary material Appendix 4).

Complete data were collected on 82 pregnant adult females shot during four hunting seasons (2001, 2002, 2005 and 2007) at Castelporziano. No shot juvenile female was pregnant in that population (Servanty et al. 2011). In Châteauvillain-Arc-en-Barrois, complete data have been collected on 226 juvenile and 506 adult females during all hunting seasons between 1983 and 2014.

Mast production data

In Castelporziano, mast production was measured through the acorn production between 2000 and 2007 (except in 2003). Between October and February, traps were located under one oak tree at about two-thirds the distance between the trunk and the canopy margin, where acorn production is the highest. Each trap consisted of a 1 m^2 iron ring enclosed by a small fence to prevent ungulate depredation of captured acorns. There was no protection against jays and rodents (Focardi et al. 2008). Up to fifty traps were distributed within the preserve. Each year, an acorn production index was calculated as the average number of acorns collected per trap (see Focardi et al. 2008 for further details about the procedure) (Fig. 2a). It is noteworthy that this index fluctuated a lot during the study period (Fig. 2a). In the following analyses, mast production was entered as a continuous variable at Castelporziano.

In Châteauvillain-Arc-en-Barrois, mast production was measured between 1983 and 2014 based on diet composition obtained from the analysis of stomach contents during the hunting period (Brandt et al. 2006). We identified four categories of years depending on the quantity of acorns and beechnuts found in the stomachs: acorn-mast years (*A*) when acorns represented 75–90% of stomach contents, years of medium acorn production (*AA*) when acorns represented 50–65% of stomach contents, beechnut-mast years (*B*) when beechnuts represented 65–85% of stomach contents and years with no mast production (*N*) when acorns or beechnuts represented less than 3% (see Servanty et al. (2009) for further details). Hence, in Châteauvillain-Arc-en-Barrois, years may differ in terms of fruit quantity and they can also differ in terms of type of fruits produced (i.e., acorns vs. beechnuts) (Fig. 2b). It is noteworthy that acorn and beechnut productions are not synchronized (see Fig. 2b) making food resources almost consistently available for wild boar.

As a given hunting season encompassed two civil years, we defined a year based on seasonality of the seed availability. Thus, a new year started on October 1st (Fig. 1).

Path analyses

We expected that different kinds of seeds may generate variation in female body mass. More specifically, the intensity of fruit production (hereafter called seed availability) in the current year t (P_t), in the previous year $t - 1$ (P_{t-1}) and in both current and previous years could potentially influence female body mass at year t. Using confirmatory path analyses (Shipley 2009, 2013), we assessed whether the variation in number of *corpora lutea* (fertility) and number of fetuses (litter size): (1) depended on female body mass only; (2) depended on the direct effect of seed availability; or (3) depended on both the direct and the indirect (i.e., operating via female body mass) effects of seed availability. We applied the Shipley's test of directed separation (Shipley 2009, 2013) for identifying the most likely scenario.

First, we fitted the global path model including all the possible effects. This model included the effects of the seed availability in the current year t (P_t) and in the previous year $t - 1$ (P_{t-1}) on female body mass and also on reproductive traits (i.e., fertility and litter size), the effects of female body mass on fertility and on litter size and the effect of fertility on litter size. Therefore, the path model consisted of three linear relationships implemented with the lm function: one linking female body mass as a response variable to previous and current seed availability, one linking fertility as a response variable to female body mass and (previous and current) seed availability, and one linking litter size as a response variable to fertility, female body mass and (previous and current) seed availability. The minimal path model we fitted included the effect of seed availability (either the current P_t or the previous year P_{t-1}) on female body mass only, which in turn influenced fertility, and thereby litter size. We fitted all the 96 possible models derived from the global path model. We used the Akaike Information Criterion corrected for small sample size (AICc) for model selection (Shipley 2013). We calculated the Fisher's C statistic of the path model retained as well as the Chi squared test degrees of freedom. The C statistic should follow a Chi squared distribution if the data are effectively generated following the cause-order effect modeled in the path model (Shipley 2009, 2013). Moreover, we recovered the standardized regression coefficients (scaled by mean and variance) and their associated SE.

We conducted separate path analyses for the two populations because marked between-population differences in the type of fruit production and in the ecological context led us to expect differences in allocation patterns to reproduction. Likewise, we also conducted separate path analyses for juveniles and adults because juvenile females still have to allocate a large amount of resources to growth (Servanty et al. 2009; Gamelon et al. 2013), whereas most adult females have reached their asymptotic mass. Milner et al. (2014) have recently highlighted that artificial feeding might influence ungulates through their fecundity. Therefore, at Castelporziano, we also tested for a potential effect of supplemental feeding (in kg) provided for summer counts on reproductive allocation (see Supplementary material Appendix 1, Table A1). We performed all analyses with R 2.12.2 (R Development Core Team 2011) using the package "piecewiseSEM" (Lefcheck 2016).

Results

Effect of seed availability on allocation to reproduction in adult females

At Castelporziano, the top two path models provided very similar fit (Table 1a, ΔAICc $= 0.29$ between models 1 and 2). The best model (Table 1a, AICc $= 28.181$) included a direct positive effect of current seed availability on fertility and a negative effect on litter size. Also, the current seed availability had a slight positive effect on female body mass, and we found the expected positive effects of female body mass on fertility and of fertility on litter size (Fig. 3a, first path model, Supplementary material Appendix 5, Table A2). This model satisfactorily fitted the data based on comparison of the Fisher's C statistic to a Chi squared distribution ($C_2 = 2.41$, $p = 0.3$). Thus, this model predicts a live body mass of 62.85 kg for a year of low seed availability (vs. 67.72 kg for a year of abundant seed availability), a fertility of 4.48 *corpora lutea* (vs. 5.28 for a year of abundant seed availability) and a litter size of 4.39 fetuses (vs. 3.80 for a year of abundant seed availability) (Table 2, Supplementary material Appendix 6, Table A3). From this selected model, an additional relationship between supplemental feeding and female body mass was close to statistical significance but negative (−0.23 (SE 0.12), $p = 0.05$). Likewise, from this best model, replacing the effect of current seed availability with supplemental feeding did not point out any pathways between supplemental feeding and female body mass (−0.14 (SE 0.11), $p = 0.22$), between supplemental feeding and fertility (−0.01 (SE 0.11), $p = 0.92$), and between supplemental feeding and litter size (−0.17 (SE 0.11), $p = 0.11$). The other top path model (Table 1a, AICc $= 28.471$) also fitted the data well

Table 1 Model fit of the different competing path models

Model notation	N	AICc	ΔAICc
(a)			
(1) $M \sim P_t/C \sim M + P_t/F \sim C + P_t$	**11**	**28.181**	**0**
(2) $M \sim P_{t-1}/C \sim M + P_{t-1}/F \sim C + P_{t-1}$	**11**	**28.471**	**0.29**
$M \sim P_{t-1}/C \sim M + P_{t-1}/F \sim C + P_t$	11	31.461	3.28
$M \sim P_{t-1}/C \sim M + P_{t-1}/F \sim C + P_t + M$	12	31.692	3.511
$M \sim P_{t-1}/C \sim M + P_{t-1}/F \sim C$	10	31.739	3.558
(b)			
$M \sim P_t/C \sim M + P_t/F \sim C + M$	**15**	**31.51**	**0**
$M \sim P_{t-1}/C \sim M/F \sim C + M$	12	33.523	2.013
$M \sim P_{t-1}/C \sim M + P_{t-1}/F \sim C + M$	15	33.86	2.35
$M \sim P_t/C \sim M + P_t/F \sim C$	14	35.405	3.895
$M \sim P_{t-1}/C \sim M/F \sim C$	11	36.684	5.174
(c)			
$M \sim P_{t-1}/C \sim M/F \sim C$	**11**	**27.924**	**0**
$M \sim P_{t-1}/C \sim M/F \sim C + M$	12	28.985	1.061
$M \sim P_{t-1}/C \sim M + P_{t-1}/F \sim C$	14	32.031	4.107
$M \sim P_{t-1}/C \sim M + P_{t-1}/F \sim C + M$	15	33.156	5.232
$M \sim P_{t-1}/C \sim M/F \sim C + P_{t-1}$	14	33.991	6.067

These models derived from the global path model that explores the relationship between seed availability (during current P_t and previous P_{t-1} year), female body mass M, fertility (measured by the number of *corpora lutea* C) and litter size (measured by the number of fetuses F)

Displayed are the number of parameters (N), the AICc of the five best models, and the difference between each tested model and the best one (ΔAICc) for (a) adult wild boar females in Castelporziano, Italy ($n = 82$); (b) adult wild boar females in Châteauvillain-Arc-en-Barrois, France ($n = 506$); and (c) juvenile wild boar females in Châteauvillain-Arc-en-Barrois, France ($n = 226$). The models retained are indicated in bold

($C_2 = 2.7$, $p = 0.26$). Comparing these top two models indicates that abundant current (Fig. 3a, first path model) and previous (Fig. 3a, second path model) seed availability had basically the same effect on female body mass and reproductive traits. This second model predicts a live body mass of 60.38 kg when the previous year was characterized with a low seed availability (vs. 68.64 kg for a previous year of abundant seed availability), a fertility of 4.27 *corpora lutea* (vs. 5.31 for a previous year of abundant seed availability) and a litter size of 4.25 fetuses (vs. 3.96 for a previous year of abundant seed availability) (Table 2, Supplementary material Appendix 5, Table A2). From this selected model, an additional relationship between supplemental feeding and female body mass was not significant (−0.08 (SE 0.11), $p = 0.46$).

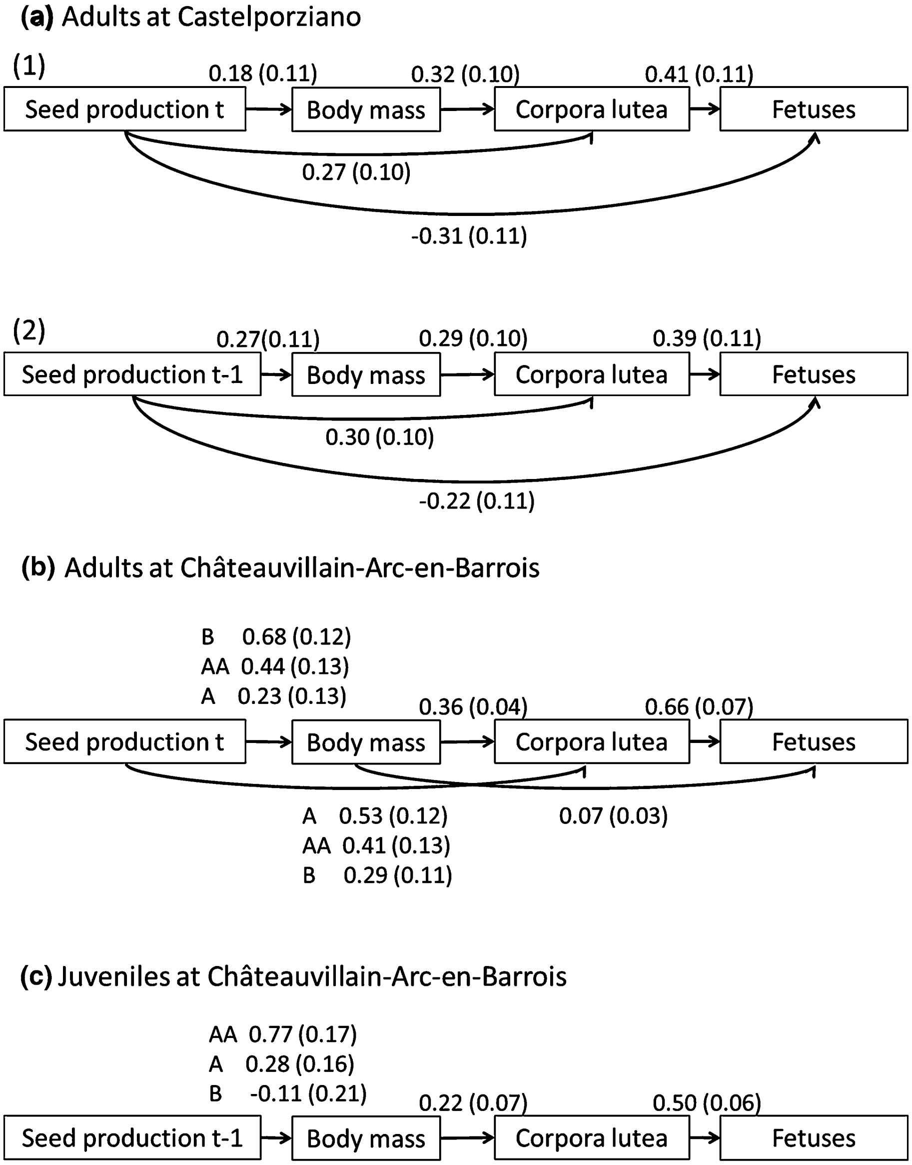
At Châteauvillain-Arc-en-Barrois, the top path model for adult females (Table 1b, AICc = 31.51) satisfactorily fitted the data ($C_2 = 0.53$, $p = 0.769$). This model included direct strong positive effects of the amount of acorns (categories denoted *A* and *AA*, Fig. 3b) and beechnuts (at a lesser extent, category *B*) on fertility of adult females. On the other hand, high current beechnut production strongly increased female body mass, whereas the positive effect of acorn production on body mass was much weaker. Body mass was directly positively linked to fertility and litter size, and fertility was positively associated with litter size (Fig. 3b, Supplementary material Appendix 5, Table A2). As an illustration, this model predicts a dressed body mass of 50.34 kg (corresponding to a live body mass of about 64 kg) for a non-mast year (vs. 55.61 kg (i.e., a live body mass of about 70 kg) for a year of medium acorn production and 58.41 kg (i.e., a live body mass of about 73 kg) for a beechnut-mast year), a fertility of 5.88 *corpora lutea* (vs. 6.90 for a year of medium acorn production and 6.83 for a beechnut-mast year) and a litter size of 5.21 fetuses (vs. 5.94 for a year of medium acorn production and 5.93 for a beechnut-mast year) (Table 2, Supplementary material Appendix 6, Table A3).

The comparison between the path models retained in Castelporziano (Fig. 3a) and Châteauvillain-Arc-en-Barrois (Fig. 3b) reveals some common patterns. In both areas, adult female body mass increased with current seed availability and positively influenced fertility, measured as the number of *corpora lutea*, with similar effect sizes in both populations. An increased fertility led to larger litter sizes. In addition, in both areas, the fertility of adult wild boar females directly increased with current seed availability. However, some discrepancies also occurred between the two populations. Litter size in the Italian population decreased with increasing current or previous seed availability. On the contrary, litter size in the French population increased with female body mass. In the resource-limited population, previous and current seed availability had similar effects on female body mass and reproductive traits, whereas in the population facing abundant resources, only the current seed availability mattered.

Effect of seed availability on allocation to reproduction in juvenile females

At Châteauvillain-Arc-en-Barrois, a substantial proportion of juvenile females reproduced. Contrary to what we found in adults, current seed availability never showed up in the top path models for juveniles and all the competitive models included an effect of previous seed availability (Table 1c). The top path model (Table 1c, AICc = 27.924) satisfactorily fitted the data ($C_6 = 4.69$, $p = 0.585$). Both previous acorn-mast year and previous year of medium acorn production positively influenced body mass of juvenile females. On the contrary, previous beechnut-mast year had virtually no effect on body mass. Like in adults, heavier juvenile females had higher fertility, and a high fertility was positively associated with litter size (Fig. 3c,

Fig. 3 Selected path models (see Table 1) showing how seed availability the current P_t or the previous P_{t-1} year may directly and/or indirectly influence female body mass, fertility (measured by the number of *corpora lutea*), and litter size (measured by the number of fetuses) produced by **a** adult wild boar females in Castelporziano, Italy; **b** adult wild boar females in Châteauvillain-Arc-en-Barrois, France; and **c** juvenile wild boar females in Châteauvillain-Arc-en-Barrois, France. For each relationship, standardized coefficients and their associated SE are given. Note that for (**b**) and (**c**), standardized coefficients for the effect of seed availability (*A* acorn-mast year, *AA* year of medium acorn production, *B* beechnut-mast year) are given relatively to non-mast year (both low acorn and beechnut production)



Supplementary material Appendix 5, Table A2). Thus, this model predicts a dressed body mass of 32.85 kg (corresponding to a live body mass of about 42 kg) for a non-mast year (vs. 36.86 kg (i.e., a live body mass of about 47 kg) for a year of medium acorn production and 32.29 kg (i.e., a live body mass of about 41 kg) for a beechnut-mast year), a fertility of 4.92 *corpora lutea* (vs. 5.10 for a year of medium acorn production and 4.89 for a beechnut-mast year) and a litter size of 4.05 fetuses (vs. 4.17 for a year of medium acorn production and 4.03 for a beechnut-mast year) (Table 2, Supplementary material Appendix 6, Table A3). Remarkably, previous seed availability affected reproductive traits only through the indirect pathway (i.e., through female body mass).

Discussion

This comparative study of two wild boar populations facing with markedly different amount of resources and hunting pressure indicates some common patterns in the way wild boar females, which are pulsed-resource consumers, allocate resources to reproduction. Our findings also provide clear evidence that females are able to display different age-specific and context-dependent breeding tactics to cope with highly variable food resources. The plasticity in breeding tactics both between and within populations may be a key feature of wild boar life history.

Table 2 Predicted values of female live body mass (M, in kg) and dressed body mass (into parentheses), fertility (measured by the number of *corpora lutea* C) and litter size (measured by the number of fetuses F) for (a) adults at Castelporziano, Italy, (b) adults at Châteauvillain-Arc-en-Barrois, France, and (c) juveniles at Châteauvillain-Arc-en-Barrois, France, under different conditions of seed availability

	Low P_t	High P_t		
(a) Adults at Castelporziano (1)				
Female body mass M	62.85	67.72		
Fertility C	4.48	5.28		
Litter size F	4.39	3.80		
	Low P_{t-1}	High P_{t-1}		
Adults at Castelporziano (2)				
Female body mass M	60.38	68.64		
Fertility C	4.27	5.31		
Litter size F	4.25	3.96		
	N_t	A_t	AA_t	B_t
(b) Adults at Châteauvillain-Arc-en-Barrois				
Female body mass M	64 (50.34)	67 (53.03)	70 (55.61)	73 (58.41)
Fertility C	5.88	6.78	6.90	6.83
Litter size F	5.21	5.82	5.94	5.93
	N_{t-1}	A_{t-1}	AA_{t-1}	B_{t-1}
(c) Juveniles at Châteauvillain-Arc-en-Barrois				
Female body mass M	42 (32.85)	44 (34.33)	47 (36.86)	41 (32.29)
Fertility C	4.92	5.14	5.10	4.89
Litter size F	4.05	4.17	4.17	4.03

At Castelporziano, predictions were calculated from the two best models retained (see Table 1 and Supplementary material Appendix 6, Table A3) considering the lowest and the highest intensities of acorn production (the current P_t or the previous P_{t-1} year) observed during the study period. At Châteauvillain-Arc-en-Barrois, predictions were calculated from the best models retained (see Table 1 and Supplementary material Appendix 6, Table A3) with seed availability divided into N non-mast year, A acorn-mast year, AA year of medium acorn production and B beechnut-mast year

Past versus current seed availability and breeding tactics

According to the current life history theory, wild boar should store resources acquired prior to the reproductive period for future reproduction in response to low and unreliable resource availability, and display thereby a capital breeding tactic (Drent and Daan 1980; Jönsson 1997). In accordance, capital breeding tactic has commonly been reported in most large vertebrates living in seasonal temperate ecosystems (Festa-Bianchet et al. 1998). Reproductive allocation patterns we identified in adult females at Castelporziano partially match this expectation. The relative influence of seed availability during the previous fall and during the current year was equally important for shaping the reproductive output of wild boar females (Fig. 3a), which indicates that resource-limited wild boar females occupy an intermediate position along the capital-income continuum of breeding tactics. On the contrary, adult wild boar females at Châteauvillain-Arc-en-Barrois only allocated current resources to reproduction (Fig. 3b), which indicates that wild boar females do not rely on stored energy for reproduction when facing with abundant resources. Therefore, contrary to the expectation, adult females in the French study area ranked close to the income end of the capital-income continuum of breeding tactics (Drent and Daan 1980; Jönsson 1997).

While pulsed resources were unpredictable in both study areas, forest productivity was much higher in the French than in the Italian (resource-limited) site. The rich habitat made resources for wild boar almost not limited in Châteauvillain-Arc-en-Barrois (Servanty et al. 2009, 2011), which could have favored an income breeding tactic (Jönsson 1997; Stephens et al. 2014). Such an income breeder tactic in the French population might also be explained in light of wild boar life history strategy. Indeed, a comparative demographic analysis between these two populations has revealed that wild boar at Castelporziano displayed a demographic pattern close to that of other long-lived species (Servanty et al. 2011) besides a much higher annual fecundity (Focardi et al. 2008). On the contrary, wild boar at Châteauvillain-Arc-en-Barrois have a much faster life cycle in response to the especially high hunting pressure (Gamelon et al. 2011). Thus, wild boar females in the French population give birth at a young age (one year of age instead of two years of age, Servanty et al. 2009), to a large number of offspring (Servanty et al. 2011) and have short lifespan (Toïgo et al. 2008; Servanty et al. 2009). Accordingly, generation time, which measures the position of a given population or species on the slow-fast continuum of life history variation (Gaillard et al. 2005; see also Gaillard et al. 2016 for a recent review), was very short (2 years) in this heavily hunted population, being closer to generation times observed in small passerines than to those commonly reported in ungulates (Servanty et al. 2011). Under such extreme conditions, most wild boar females only have one or two reproductive attempts on average (Gamelon et al. 2011). In that context, the income breeding tactic could have been favored to avoid costs of storing resources (Jönsson 1997). Indeed, capital breeding requires that resources are stored, which is energetically costly (Jönsson 1997). Moreover, it has been shown that fat stores may potentially reduce locomotion (Andersson and Norberg 1981) and thus the ability to escape predators leading to obvious demographic costs. It thus makes sense that in a context of high hunting pressure, the income breeding tactic has been favored in the French population.

Seed availability and its effects on reproductive traits

Although seed availability positively influenced the reproductive output of adult females in both populations, this effect occurred through multiple pathways. Abundant seed availability led to direct increase of fertility, indicating that wild boar females adjust their reproductive output to resource availability. In addition, abundant seed availability influenced fertility in an indirect way, by increasing female body mass, indicating that fertility in wild boar is mass dependent, like in most mammals studied so far (Bronson 1989; Heard et al. 1997; Fernández-Llario and Mateos-Quesada 1999). As expected, litter size, measured as the number of fetuses, was positively related to female fertility, measured as the number of *corpora lutea*. This set of relationships shows that abundant seed availability improves female body mass and both absolute and relative (to female body mass) allocation to reproduction in the two studied populations (Fig. 3a, b).

The strength of the relationship linking fertility and litter size (Fig. 3, see also Supplementary material Appendix 3, Fig. A2, solid lines) was higher in Châteauvillain-Arc-en-Barrois than in Castelporziano, which may indicate a lower embryonic mortality in the French population. In this latter population, the direct positive effect of female body mass on litter size provides further evidence for reduced embryonic mortality in heavy females compared to light ones (Abaigar 1992). Likewise, the strength of the relationship linking fertility and litter size was lower in juveniles than in adults at Châteauvillain-Arc-en-Barrois, which indicates that the embryonic mortality was higher in young than in adult females (Fig. 3c). Somewhat counter-intuitive at first sight in the Italian population, the direct effect of both past and current seed availability on litter size was negative, indicating that embryonic mortality increased with the intensity of seed production (Fig. 3a). When the seed availability is important, the number of *corpora lutea* increases. In that context, we might expect embryonic mortality to offer a pathway for pregnant females to adjust litter size to available resources via selective abortion (Birney and Baird 1985; Gosling 1986) and limit thereby the high costs associated with lactation in polytocous species such as wild boar (Oftedal 1985; Clutton-Brock 1991) in highly variable environments. Further works will be required to assess the potential role of selective abortion in reproductive tactics. In addition, some potential climate effects (e.g., severe droughts) on embryonic mortality in the Italian study site cannot be excluded.

Quantity and type of fruit production

Previous seed availability mattered for juvenile females but not for adult females in the French population and the entire effect of mast production on reproduction of juvenile wild boar females was indirect through body mass (Fig. 3c). Importantly, previous seed availability (i.e., in autumn at year $t - 1$) benefits mothers that give birth in spring of that year $t - 1$ (Fig. 1) by allowing them to produce offspring with enhanced growth and/or larger birth mass (see Kjellander et al. 2006 for an empirical evidence for heavier fawns produced after an acorn-mast year in roe deer *Capreolus capreolus*). Females in the French population only need to reach about 33–41% of the asymptotic adult body mass in autumn at year t to reproduce (Servanty et al. 2009). It is likely that the high hunting pressure that has been in place for more than 30 years (see Gamelon et al. 2011) and that acted on several generations of wild boar (generation time equals 2.27 years, Servanty et al. 2011) has selected for early sexual maturity at a low threshold body mass (Servanty et al. 2009). Thus, females born in years with high seed availability should be heavier the next autumn during the rut and should thereby have higher fertility and larger litter size than females born in years with low seed availability. That explains why previous seed production (i.e., just prior to birth) determines the propensity of juvenile females to reproduce at Châteauvillain-Arc-en-Barrois.

Our findings also question how we should define the quality of a given year in relation to the performance (growth and reproduction) of wild boar females at

Châteauvillain-Arc-en-Barrois. In this area, years can be qualitatively split into non-mast, acorn-mast or beechnut-mast years. Acorns have high fat contents, carbohydrates, vitamins and minerals (Goodrum et al. 1971; Short and Epps 1976). Importantly, acorns also contain lysine, an essential amino acid that is a primary determinant of lactation performance for females of domestic pigs (Yang et al. 2000). The lysine concentration in female diet determines offspring growth (Yang et al. 2000). Therefore, females born in an acorn-mast year should benefit from rich milk favoring offspring growth, leading to increase reproductive performance the subsequent year compared to females born in years without acorns (Fig. 3c). Therefore, the type of the mast production (acorn vs. beechnut) does matter for growth and reproduction. A better knowledge of the lysine concentration of both acorns and beechnuts is strongly needed to understand their differential effects on reproductive allocation patterns of wild boar females. The results obtained for adult females provided additional support for the differential effects of acorns and beechnuts in reproduction. Indeed, while acorns directly influenced fertility, the effect of beechnuts mainly operated indirectly via female body mass (Fig. 3b). Importantly, fat (respectively, protein) content in beechnuts can be more than 11 times (respectively, more than 22 times) higher than in acorns (Fietz et al. 2005). To what extent these high fat and protein contents in beechnuts contribute to heavier female body mass definitely requires further detailed physiological studies and offers promising avenues of research. This finding stresses the importance of accounting for both quantity and type of mast production to understand how pulsed resources are allocated to reproductive traits.

Conclusions

From the analyses of wild boar populations subjected to highly different environmental contexts, we demonstrated that the frequency of pulsed resources definitely shapes the high reproductive output (Massei et al. 1996) of that large polytocous mammal. Female wild boar cope efficiently with ephemeral resources by adjusting their reproductive allocation in relation to their age and to the ecological context.

Our findings allow drawing some general recommendations for the study of allocation to reproduction in variable environments. First, pulsed resources should be precisely defined both in terms of quantity and type of fruit produced because heterogeneity in the nutritive content of seeds across tree species might alter the effect of a given amount of seeds on reproductive allocation. In addition, it is important to keep in mind that resources are allocated to reproductive traits through different pathways. Therefore, for a full understanding of the underlying mechanisms of allocation to reproduction, carefully disentangling direct and indirect effects of pulsed resources on reproductive traits is badly required. In that context, path analyses offer a useful and straightforward approach (Lefcheck 2016). Finally, investigations of the way a pulsed-resource consumer allocates resources to reproduction should account for potential age specificity and context dependency.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

References

Abaigar T (1992) Paramètres de la reproduction chez le sanglier (*Sus scrofa*) dans le sud-est de la Péninsule Ibérique. Mammalia 56:245–250

Abrams PA (1990) Adaptive responses of generalist herbivores to competition: convergence or divergence. Evol Ecol 4:103–114. doi:10.1007/BF02270908

Albon SD, Mitchell B, Huby BJ, Brown D (1986) Fertility in female Red deer (*Cervus elaphus*): the effects of body composition, age and reproductive status. J Zool 209:447–460. doi:10.1111/j.1469-7998.1986.tb03603.x

Andersson M, Norberg RÅ (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biol J Linn Soc 15:105–130. doi:10.1111/j.1095-8312.1981.tb00752.x

Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. J Appl Ecol 42:1203–1213. doi:10.1111/j.1365-2664.2005.01094.x

Birney EC, Baird DD (1985) Why do some mammals polyovulate to produce a litter of two? Am Nat 126:136–140

Blockstein DE, Tordoff HB (1985) Gone forever: a contemporary look at the extinction of the passenger pigeon. Am Birds 39:845–851

Bogdziewicz M, Zwolak R, Crone EE (2016) How do vertebrates respond to mast seeding? Oikos 125:300–307. doi:10.1111/oik.03012

Boutin S, Wauters LA, McAdam AG, Humphries MM, Tosi G, Dhondt AA (2006) Anticipatory reproduction and population growth in seed predators. Science 314:1928–1930. doi:10.1126/science.1135520

Brandt S, Baubet E, Vassant J, Servanty S (2006) Régime alimentaire du sanglier en milieu forestier de plaine agricole. Faune Sauvage 273:20–27

Bronson FH (1989) Mammalian reproductive biology. University of Chicago Press, Chicago

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252

Fernández-Llario P, Mateos-Quesada P (1999) Body size and reproductive parameters in the wild boar *Sus scrofa*. Acta Theriol (Warsz) 43:439–444

Festa-Bianchet M, Gaillard J-M, Jorgenson JT (1998) Mass-and density-dependent reproductive success and reproductive costs in a capital breeder. Am Nat 152:367–379

Fietz J, Pflug M, Schlund W, Tataruch F (2005) Influences of the feeding ecology on body mass and possible implications for reproduction in the edible dormouse (*Glis glis*). J Comp Physiol B 175:45–55. doi:10.1007/s00360-004-0461-1

Focardi S, Gaillard J-M, Ronchi F, Rossi S (2008) Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. J Mammal 89:1113–1123. doi:10.1644/07-MAMM-A-164.1

Franzetti B, Ronchi F, Marini F, Scacco M, Calmanti R, Calabrese A, Paola A, Paolo M, Focardi S (2012) Nocturnal line transect sampling of wild boar (*Sus scrofa*) in a Mediterranean forest: long-term comparison with capture–mark–resight population estimates. Eur J Wildl Res 58:385–402. doi:10.1007/s10344-011-0587-x

Gaillard J-M, Sempéré AJ, Boutin J-M, Laere GV, Boisaubert B (1992) Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). Can J Zool 70:1541–1545. doi:10.1139/z92-212

Gaillard J-M, Yoccoz NG, Lebreton J-D, Bonenfant C, Devillard S, Loison A, Pontier D, Allaine D (2005) Generation time: a reliable metric to measure life-history variation among mammalian populations. Am Nat 166:119–123

Gaillard J-M, Lemaître J-F, Berger V, Bonenfant C, Devillard S, Douhard M, Gamelon M, Plard F, Lebreton J-D (2016) Axes of variation in life histories. Encyclopedia of evolutionary biology. Elsevier, Oxford, pp 312–323

Gamelon M, Besnard A, Gaillard J-M, Servanty S, Baubet E, Brandt S, Gimenez O (2011) High hunting pressure selects for earlier birth date: wild boar as a case study. Evolution 65:3100–3112. doi:10.1111/j.1558-5646.2011.01366.x

Gamelon M, Douhard M, Baubet E, Gimenez O, Brandt S, Gaillard J-M (2013) Fluctuating food resources influence developmental plasticity in wild boar. Biol Lett 9:20130419. doi:10.1098/rsbl.2013.0419

Gerhart KL, Ruussell DE, Wetering DVD, White RG, Cameron RD (1997) Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. J Zool 242:17–30. doi:10.1111/j.1469-7998.1997.tb02926.x

Goodrum PD, Reid VH, Boyd CE (1971) Acorn yields, characteristics, and management criteria of oaks for wildlife. J Wildl Manag 35:520–532. doi:10.2307/3799707

Gosling LM (1986) Selective abortion of entire litters in the coypu: adaptive control of offspring production in relation to quality and sex. Am Nat 127:772–795

Heard D, Barry S, Watts G, Child K (1997) Fertility of female moose (*Alces alces*) in relation to age and body composition. Alces 33:165–176

Hewison AJM, Gaillard JM (2001) Phenotypic quality and senescence affect different components of reproductive output in roe deer. J Anim Ecol 70:600–608. doi:10.1046/j.1365-2656.2001.00528.x

Holt RD (2008) Theoretical perspectives on resource pulses. Ecology 89:671–681. doi:10.1890/07-0348.1

Jedrzejewska B, Jedrzejewski W, Bunevich AN, Milkowski L, Krasinski ZA (1997) Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriol (Warsz) 42:399–451

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66. doi:10.2307/3545800

Kjellander P, Gaillard J-M, Hewison AJM (2006) Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia 146:521–530. doi:10.1007/s00442-005-0188-z

Koenig WD, Díaz M, Pulido F, Alejano R, Beamonte E, Knops JMH (2013) Acorn production patterns. In: Campos P, Huntsinger L, Pro JLO, Starrs PF, Diaz M, Standiford RB, Montero G (eds) Mediterranean oak woodland working landscapes. Springer, Amsterdam, pp 181–209

Lefcheck JS (2016) piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol Evol. doi:10.1111/2041-210X.12512

Massei G, Genov PV (2004) The environmental impact of wild boar. Galemys Bol Inf Soc Esp Para Conserv Estud Los Mamíferos 16:135–145

Massei G, Genov PV, Staines BW (1996) Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. Acta Theriol (Warsz) 41:307–320

Matschke GH (1964) The influence of oak mast on European wild hog reproduction. In: 18th Conference of South-eastern Association Game and Fish Commission. Clearwater, Florida, pp 35–39

Matschke GH (1967) Aging European wild hogs by dentition. J Wildl Manag 31:109–113. doi:10.2307/3798365

McDonald JE, Fuller TK (2005) Effects of spring acorn availability on black bear diet, milk composition, and cub survival. J Mammal 86:1022–1028. doi:10.1644/1545-1542(2005)86[1022:EOSAAO]2.0.CO;2

Milner JM, Van Beest FM, Schmidt KT, Brook RK, Storaas T (2014) To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. J Wildl Manag 78:1322–1334. doi:10.1002/jwmg.798

Oftedal OT (1985) Pregnancy and lactation. In: Hudson RJ, White RG (eds) Bioenergetics of wild herbivores. CRC Press, Boca Raton, pp 215–238

Ostfeld RS, Keesing F (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends Ecol Evol 15:232–237. doi:10.1016/S0169-5347(00)01862-0

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Schmidt KA (2003) Linking frequencies of acorn masting in temperate forests to long-term population growth rates in a songbird: the veery (*Catharus fuscescens*). Oikos 103:548–558. doi:10.1034/j.1600-0706.2003.12462.x

Servanty S, Gaillard J-M, Toïgo C, Brandt S, Baubet E (2009) Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. J Anim Ecol 78:1278–1290. doi:10.1111/j.1365-2656.2009.01579.x

Servanty S, Gaillard J-M, Ronchi F, Focardi S, Baubet E, Gimenez O (2011) Influence of harvesting pressure on demographic tactics:

implications for wildlife management. J Appl Ecol 48:835–843. doi:10.1111/j.1365-2664.2011.02017.x

Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368. doi:10.1890/08-1034.1

Shipley B (2013) The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94:560–564. doi:10.1890/12-0976.1

Short HL, Epps EA (1976) Nutrient quality and digestibility of seeds and fruits from Southern forests. J Wildl Manag 40:283–289. doi:10.2307/3800427

Stephens PA, Houston AI, Harding KC, Boyd IL, McNamara JM (2014) Capital and income breeding: the role of food supply. Ecology 95:882–896. doi:10.1890/13-1434.1

Toïgo C, Servanty S, Gaillard J-M, Brandt S, Baubet E (2008) Disentangling natural from hunting mortality in an intensively hunted wild boar population. J Wildl Manag 72:1532–1539. doi:10.2193/2007-378

Yang H, Pettigrew JE, Johnston LJ, Shurson GC, Walker RD (2000) Lactational and subsequent reproductive responses of lactating sows to dietary lysine (protein) concentration. J Anim Sci 78:348–357. doi:10.2527/2000.782348x

Yang LH, Bastow JL, Spence KO, Wright AN (2008) What can we learn from resource pulses? Ecology 89:621–634. doi:10.1890/07-0175.1

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Understory vegetation dynamics and tree regeneration as affected by deer herbivory in temperate hardwood forests

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Plant competition and deer browsing are two main factors which limit tree recruitment. We examined natural tree-recruitment processes under continuous-tree-cover management. Changes in plant communities and tree regeneration were monitored over an eight-year period at two different sites in a temperate hardwood forest in the North-East of France. We used paired control plot (unfenced areas, free access to deer) and exclosures (fenced areas, excluding deer) at both sites. Shade-tolerant browsing-tolerant opportunistic species (beech, *Fagus sylvatica* at site 1 and bramble, *Rubus* spp. at site 2) were present in low numbers at the beginning of the study. We found that these species used a sit-and-wait strategy, waiting for opportunities to proliferate (thinning and deer exclusion). In the exclosure at site 1, beech proliferate slowly. In the exclosure at site 2, bramble proliferated enough during the first two growing seasons to prevent tree recruitment. Thus, fencing encouraged beech sapling or bramble growth, and this growth in turn was detrimental to the richness and diversity of the plant community. The two study cases presented show that both plant competition and deer browsing can be problematic for tree recruitment. Our results further suggest that excluding deer is not sufficient to enhance the growth of browse-sensitive and moderately shade-tolerant tree species such as oaks (*Quercus petraea* and *Q. robur*).

Keywords: Understory Vegetation, Plant Interaction, Competition, Browsing, Forest Regeneration, Exclosure

Introduction

The recruitment of vigorous, high-quality trees in sufficient quantity to ensure forest regeneration is a major issue in forestry. Forest renewal can be accomplished either through artificial (seeding or planting) or natural regeneration. The latter approach conforms with the basic principles of close-to-nature forest management (CNFM – Schütz 1999) and continuous-cover forestry (CCF – Pommerening & Murphy 2004), two concepts which attempt to reconcile wood production and other ecosystem services. Selective thinning is a basic technique in such forestry approaches, and ensures that young trees have enough light for proper growth while limiting the development of a dense competitive understory (Bertin et al. 2011). Indeed, strong competition from surrounding vegetation is a major obstacle to successful natural regeneration (Balandier et al. 2006) and can affect seed germination, seedling establishment, and sapling growth and survival (Davis et al. 1999, Fotelli et al. 2002).

Deer populations in recent decades have increased exponentially in numerous regions of the Northern hemisphere (Apollonio et al. 2010). Locally, forest managers are facing increasingly challenging situations for forest regeneration due to the impact of browsing, fraying and bark stripping on the growth and survival of commercially important tree species (Olesen & Madsen 2008, Gill & Beardall 2001). Furthermore, deer exclusion by fencing is expensive and is not likely to be a universally appropriate tool to prevent deer damage. For example, Wasem & Häne (2008) reported that excluding deer did not enhance tree recruitment because understory competition from bramble increased in the exclosure due to a lack of browsing. This plant strategy has been referred to as the "sit and wait" strategy. Greenberg et al. (2001) found that a non-indigenous species (*Celastrus orbiculatus Thunb*.) in North America was able to take root and persist in undisturbed sites, then benefit from a disturbance (canopy opening) to suddenly proliferate and prevent tree recruitment. Species that are resistant or tolerant to browsing (*e.g.*, through high growth rate, stored reserves, chemical or mechanical defenses) can have a head start over other species. Deer can modify the relative competitive ability of certain plants within a plant community. Indeed, differences in palatability and abundance between two competing species may give one species a competitive advantage over the other (Moser et al. 2006).

In our study, we assessed the impact of high densities of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) on vegetation dynamics and tree recruitment. We used eight years of vegetation monitoring data from paired control-exclosure plots under continuous canopy cover in

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Tab. 1 - Description of the two sites: forest characteristics and treatments. (a): Status at the beginning of the study (2005 for site 1 and 2006 for site 2); (b): Status in 2016 based on a subsample. The number of subplots at the end of the study in 2014 are shown in brackets. The forest site type at both sites is "sessiliflorous oak woodland on low acidic soils".

Variable	Units	Species	Site 1		Site 2	
			Exclosure	Control	Exclosure	Control
No. of subplots[a]	-	-	21 (6)	21 (14)	21 (21)	60 (40)
Slope[a]	%	-	12	22	2	4
Basal area[a]	m^2 ha^{-1}	-	24	24	13	23
Basal area[b]	m^2 ha^{-1}	-	21	18	35	19
Mean height[b]	m	Beech	26.5 ± 1.6	25.7 ± 1.4	43.7 ± 0.3	23.2 ± 1.6
		Oak	29.9 ± 0.7	29.1 ± 1.1	36.4 ± 2.3	32.6 ± 1.5
Dominant diameter class[a]	cm	-	40.5 - 59.5	40.0 - 60.5	23.0 - 40.5	23.0 - 40.5
Dominant diameter class[b]	cm	-	47.5 - 67.5	47.5 - 67.5	27.5 - 47.5	27.5 - 47.5
Average age[b]	year	Beech	90	90	160	150
		Oak	100	100	140	150
Thinning regime	-	-	81 m^3 ha^{-1} removed every 6 years		68 m^3 ha^{-1} removed every 8 years	
Natura 2000 Habitat	-	-	*Milio-Fagetum* and *Merculario-Abietum*		*Luzulo-Fagetum*	

two temperate broadleaved forest sites in the North-East of France. Specifically, we tested whether deer browsing affected tree-understory vegetation interactions. Finally, we attempted to clarify the role of understory vegetation competition, browsing pressure and the interactions of these two parameters to help orient future forest management in the context of CNFM/CCF.

Materials and methods

Study area

We set up a paired control plot-exclosure field experiment in the National Hunting and Wildlife Reserve (NHWR) of "*La Petite Pierre*", a 27-km² forested area located in the Vosges Mountains in North-Eastern France (48.5° N, 7.0° E). The mean elevation is around 300 m a.s.l. The climate is continental with oceanic influences; winters are relatively mild and summers are cool (mean January and mean July temperatures are 1.3 ± 0.9 and 19.4 ± 0.7 °C, respectively - Météo France data from the Phalsbourg weather station, 10 km from *La Petite Pierre*). The mean rainfall during the study period (2005-2013) was 866 ± 43 mm per year. Poor acidic soils lie on sandstone bedrock and vegetation is of poor nutritive quality. The setup was located on two different sites whose characteristics are shown in Tab. 1. Soil type was brunisol and humus ranged from oligo-mull to hemimoder.

Tab. 2 - Yearly dynamics of the mean number of roe deer (pedestrian kilometric index according to Vincent et al. 1991) and red deer (spotlight counts according to Garel et al. 2010) observed per kilometer.

Year	Roe deer	Red deer
2005	0.33	0.65
2006	0.32	0.65
2007	0.43	0.73
2008	0.34	0.79
2009	0.3	0.72
2010	0.37	1.1
2011	0.2	0.85
2012	0.24	0.72
2013	0.15	0.71
2014	0.15	1.1

Deer populations

Roe deer and red deer are the main large herbivores, while large predators are absent from the study area. Deer populations are mainly regulated by hunting. To estimate red deer populations, spotlight counts were carried out following Garel et al. (2010); roe deer populations were monitored by the pedestrian kilometric index according to Vincent et al. (1991). We expressed the count in terms of number of deer per km to account for differences in road length. Red deer population densities (ind km^{-2}) were estimated by the relationship between spotlight counts and Capture-Mark-Recapture (CMR) data following the methodology given by Garel et al. (2010 – Tab. 2). Unfortunately, no equivalent method exists to make reliable estimates of roe deer population densities, but roe deer population is lower in the study area.

Experimental setup

Paired control plot and exclosure were used: one plot (fenced plot, hereafter "exclosure") was fenced to exclude deer while the other plot was left open to natural deer browsing (unfenced plot, hereafter "control plot"). The experiments were set up in mature beech/oak forests at two different sites (about 2.2 km apart). One pair of control-exclosure plots was established in the winter of 2005 at site 1 (1.6 ha) and in the winter of 2006 at site 2 (1.5 ha). We systematically assigned 21 circular subplots (4 m²) in each of the control and exclosure plots at site 1; at site 2, 60 circular subplots (4 m²) were established in the control plot and 30 in the exclosure. The average distance between subplots was 17.3 ± 2.1 m at site 1 and 54.7 ± 21.3 m at site 2. Fences were approximately 2.3 m tall and were maintained throughout the course of the study. At both sites, thinning was undertaken before the set-up of the experiment (Tab. 1).

Data collection

Plant cover of all vascular plant species (expressed as the relative area covered by a species in percentage) was estimated with the Braun-Blanquet 7-grade cover-abundance scale (Braun-Blanquet 1932). In addition, young trees were identified at species level and categorized as seedlings (height ≤ 15 cm) or saplings (15 cm < saplings ≤ 3 m). We also estimated density and mean height for saplings only (by species) in each subplot. These measurements were used to compare establishment and growth for the five target tree species: beech (*Fagus sylvatica*), sycamore maple (*Acer pseudoplatanus*), hornbeam (*Carpinus betulus*), sessile (*Quercus petraea*) and pedunculate oak (*Q. robur*). We combined the two oak species into a single category (hereafter "oak") since considerable hybridization between sessile and pedunculate oaks prevented us from distinguishing these two species. We collected data between May 15 and June 15 every two years from 2006 to 2014 (with one additional survey in 2005 for site 1 only). In addition, we used the Braun-Blanquet 7-grade cover-abundance scale to estimate overall plant cover at each subplot for three vegetation layers: tree layer (woody vegetation >2.0 m), shrub layer (woody vegetation 2.0-0.5 m) and herbaceous layer (woody and non woody plant species <0.5 m).

Calculation and statistical analyses

We assumed the spatial distribution of individual plants to be independent and estimated the overall plant cover following Fischer (2015). Community diversity was estimated using diversity indices calculated by taking into account all the species in the botanical surveys: species richness (S) and Piélou's equitability (J – Pielou 1966).

We chose to focus on the most common tree and plant species. We therefore excluded all rare species and retained only the species recorded with a cover of more than 2.5 % in more than 5 % of the subplots of at least one site. Thus, we restricted our analyses to the four target tree species previously mentioned (beech, sycamore maple, hornbeam and oak) and 21 understory plant species (see Tab. S1 in Supplementary material). Because understory vegetation dynamics differed between the two sites as shown by non-metric multidimensional scaling (NMDS – Oksanen et al. 2016), we performed separate analyses for each site. We acknowledge that the statistical inferences from this work have some limitations due, in part, to pseudo-replication *sensu* Hurlbert (1984). Our study should therefore be taken as a comparison between two contrasting case studies. To avoid possible over-estimates in our results, we applied more conservative non-parametric tests (Wilcoxon tests, Kruskal-Wallis rank tests) rather than parametric tests and we made restrictive use of p-values. Dunn (1964) *a posteriori* multiple comparison tests were conducted on data that varied significantly from year to year. Seedling and sapling density, sapling height and diversity index were all analyzed in the same manner. Semi-variograms were performed in order to assess the presence of any patterns of spatial auto-correlation of response variables among subplots. All the analyses were performed using the R 3.1.0 statistical package (R Core Team 2014).

Results

Deer populations

In our study area, the mean number of deer observed per kilometer was 0.32 ± 0.005 (mean ± standard error of the mean) for roe deer and 0.80 ± 0.08 for red deer, corresponding to an average of 39.6 ± 11.2 (minimum: 14.5; maximum: 105.6) red deer per km² (Garel et al. 2010). This is probably an overestimate of the overall yearly mean for local populations because migrating animals that do not live year round in the reserve were undoubtedly also counted. Albeit, Dumont et al. (2005) showed that the risk of damage to broad-leaved seedlings was high at a density of 15 hinds per km².

Composition and diversity of the plant community

Plant community composition was consistently different between site 1 and site 2 (see Fig. S1b in Supplementary material). We recorded 90 different plant species: 69 at site 1 and 68 at site 2. Forty-seven species were common to both sites. At site 1, species richness at the beginning of the experiment was lower in the control plot (3.9 ± 0.5 species; mean ± SE) than in the exclosure (8.3 ± 0.4 species), but from 2010 to 2014 richness had become similar between control and exclosure plot (about 3.7 species in 2014 – Fig. 1) with a significant decrease in species richness in the exclosure plot. At site 2, species richness was consistently lower in the control plot (6.1 ± 0.4 species) than in the exclosure (7.5 ± 0.4 species) for the first five years of the experiment; then from 2012 to 2014, the situation reversed to consistently greater richness in the control (2014: 4.5 ± 0.4 species) than in the exclosure (2014: 2.9 ± 0.2 species). In site 2, Piélou's equitability was sim-

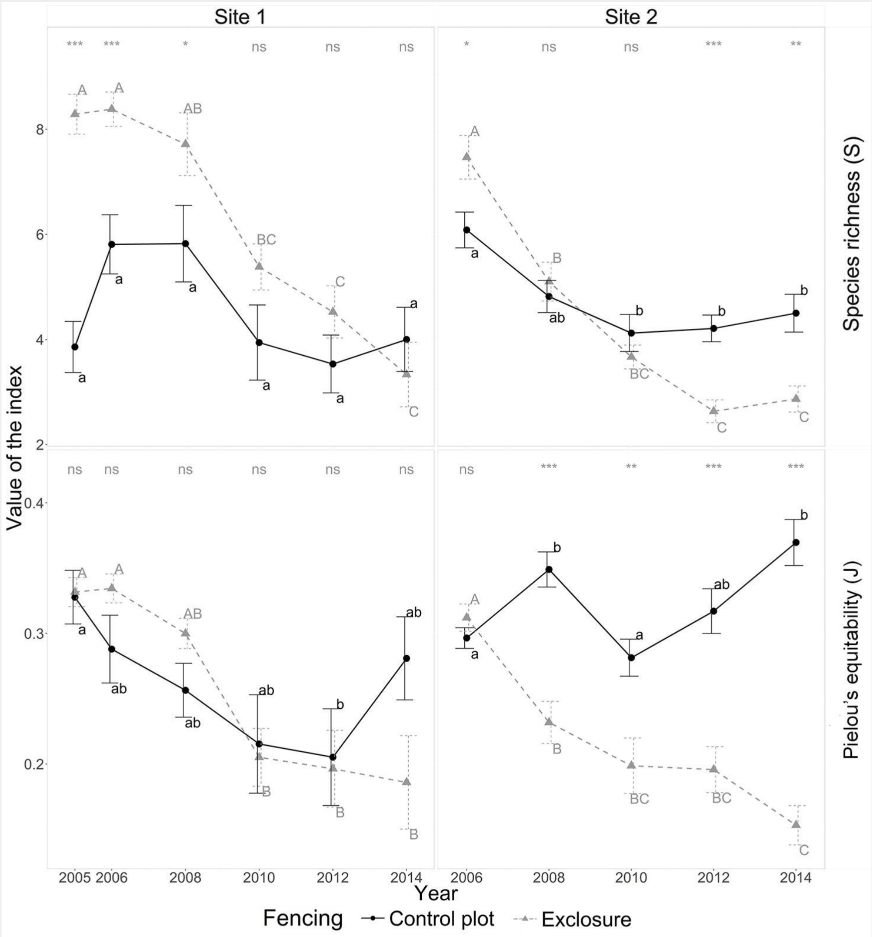


Fig. 1 - Yearly diversity index values in the presence of deer (control plot - solid line) and in the absence of deer (exclosure plot - dotted line) for sites 1 and 2 from 2005 to 2014. Error bars indicate standard errors of the mean. Wilcoxon tests were used to estimate differences between control and exclosure plots at each given year; the results of the tests are displayed at the top of each panel: (ns): non-significant; (*): p-value<0.05; (**): p-value<0.01; (***): p-value<0.001. Letters next to points indicate differences between successive years at a 5% probability (Kruskal-Wallis test): lower and upper case letters are for control and exclosure plots, respectively.

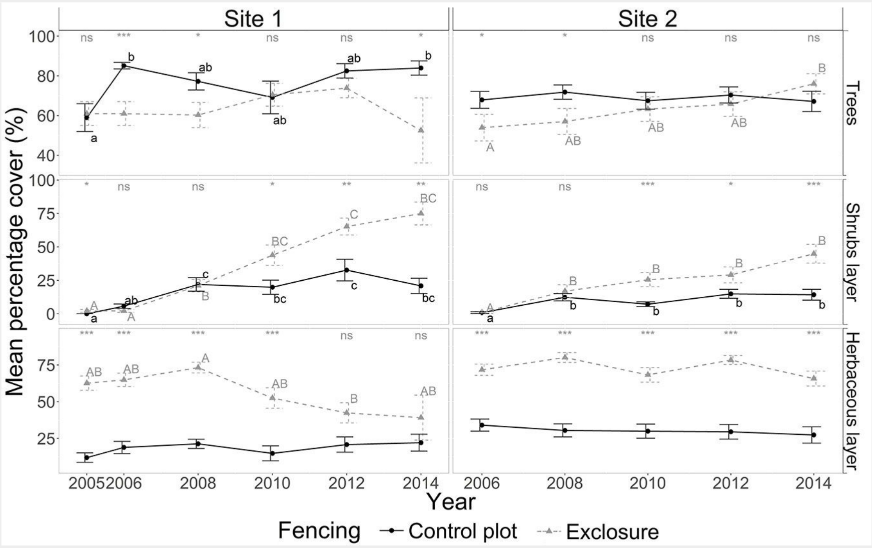


Fig. 2 - Yearly dynamics in plant cover (%) for tree, shrub and herbaceous layers in the presence of deer (control plot, solid line) and in the absence of deer (exclosure plot, dotted line) for sites 1 and 2 from 2005 to 2014. For details on the legend, see Fig. 1.

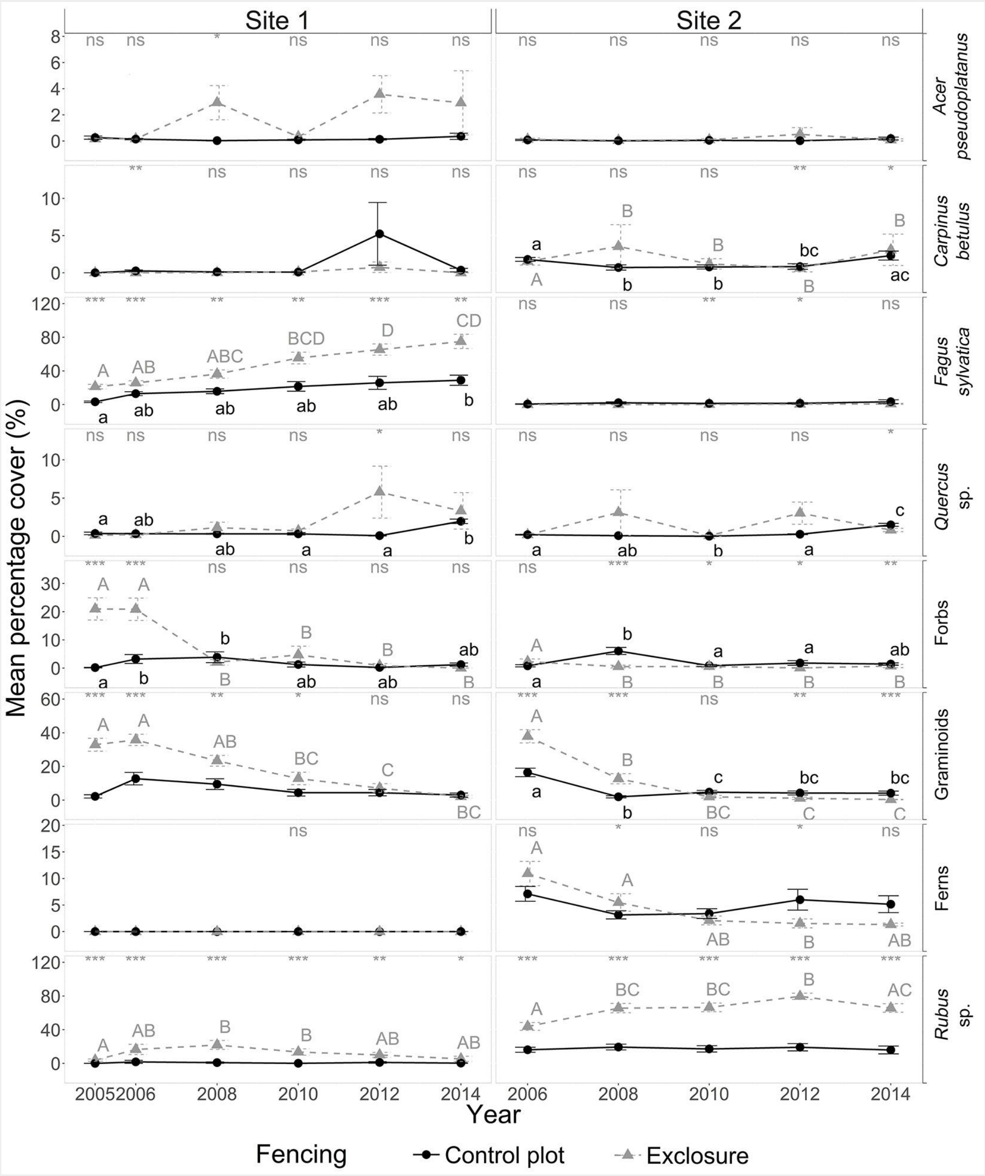


Fig. 3 - Yearly dynamics in cover (%) for the main tree, shrub and herbaceous understory species in the presence of deer (control plot, solid line) and in the absence of deer (exclosure plot, dotted line) for sites 1 and 2 from 2005 to 2014. Only species with a cover percentage greater than 2.5% in at least 5% of the sampled subplots at site 1 or 2 were considered. Note the different scales on the y axes. For details on the legend, see Fig. 1.

ilar between the control and exclosure plots at the beginning of the experiment (about 0.3). Furthermore, Piélou's equitability consistently increased in the control plot (2014: 0.37 ± 0.02) and consistently decreased in the exclosure (2014: 0.15 ± 0.02) from 2008 to 2014. Plant communities shifted toward a more complex community structure in controls and toward a simpler community structure inside the exclosure (Fig. 1). For site 2, results are consistent with NMDS results (see Fig. S1 in Supplementary material): plant communities followed different trajectories in control and exclosure plots.

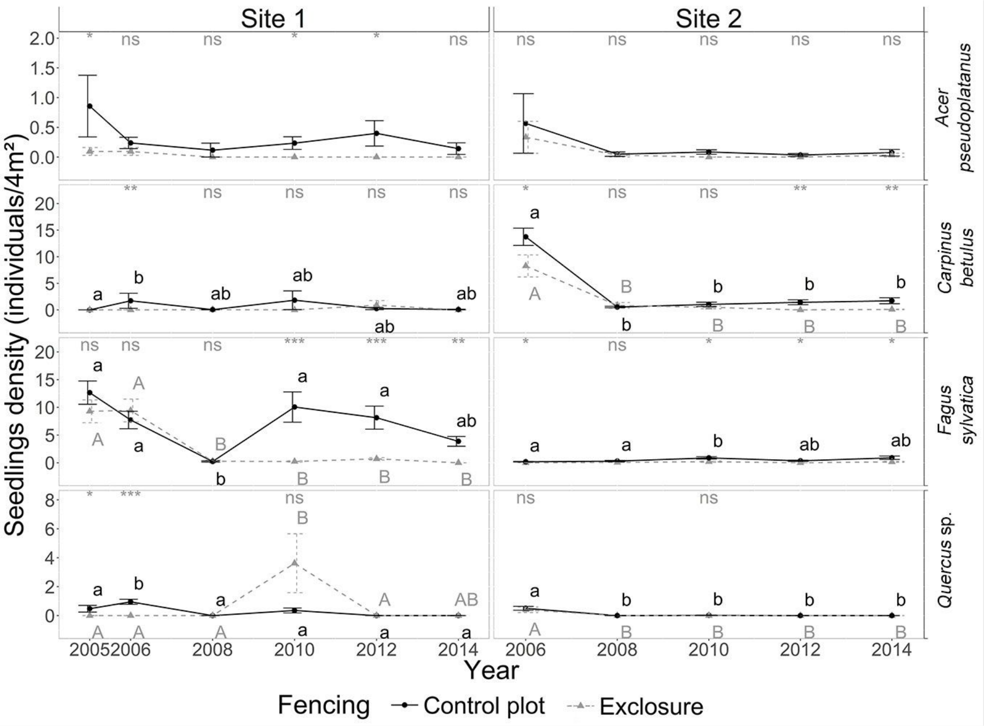
Average tree canopy cover was significantly greater (Fig. 2) in the control plot than in the exclosure at site 1 in 2006, 2008 and 2014; while no difference was observed between the control and exclosure plots the other years (2005, the beginning of the experiment, and 2010). At site 2, average tree canopy cover was significantly greater in the control plot than in the exclosure in 2006 and 2008 (Fig. 2). At both sites, shrub cover remained the same between control and exclosure plots at the beginning of the experiment (2006 - 2008), then became lower in the control plot from 2010 onwards (Fig. 2). Herbaceous cover showed different patterns at the two sites. At site 1, herbaceous plant cover decreased from 62.6 ± 4.8 % to 39.2 ± 15.3 % in the exclosure, reaching levels similar to those in the control plot (about 20 %) from 2012 onwards. At site 2, the herbaceous cover was greater in the exclosure (Fig. 2) and remained constant at about 72.8 ± 1.4 % compared to the control where it remained at about 30.5 ± 1.4 % throughout the study period.

Site 1: Beech-dominated understory

The exclusion of deer at site 1 resulted in a steady increase in beech cover from 21.3 ± 2.7 % in 2005 to 75 ± 8.5 % in 2014, while the progress in the control plot, though significant, was less pronounced (Fig. 3). It took five years to obtain a significant increase in beech cover in the exclosure plot compared to nine years in the control plot.

At site 1, tree recruitment was dominated by beech sapling dynamics; seedling and sapling densities of oak, sycamore maple and hornbeam (in decreasing order) were low – even negligible from a silvicultural point of view – in both control and exclosure plots (Fig. 4, Fig. 5). Average beech sapling density was consistently about 2.5 times lower in the control plot than in the exclosure, and remained stable over time (Fig. 5), with on average about 5.6 ± 0.2 beech saplings per square meter (Fig. 6). Beech sapling height increased from 29 ± 5 cm in 2006 to 138 ± 32 cm in 2012 in the control plot, and from 19 ± 2 cm in 2005 to 164 ± 19 cm in 2012 in the exclosure. In the exclosure, the herbaceous understory cover varied greatly over time for all three functional groups (forbs, graminoids and *Rubus* spp.) as opposed to the control plot where the herbaceous understory cover remained stable throughout the study period (Fig. 3). Graminoids showed a strong and rapid increase after fencing (35.8 ± 3.4% in

Fig. 4 - Yearly dynamics in seedling (<15 cm) density (number of seedlings per 4 m²) for the four target tree species in the presence of deer (control plot, dotted line) and in their absence (exclosure plot, solid line) for sites 1 and 2 from 2005 to 2014. Note the different scales on the y axes. For details on the legend, see Fig. 1.



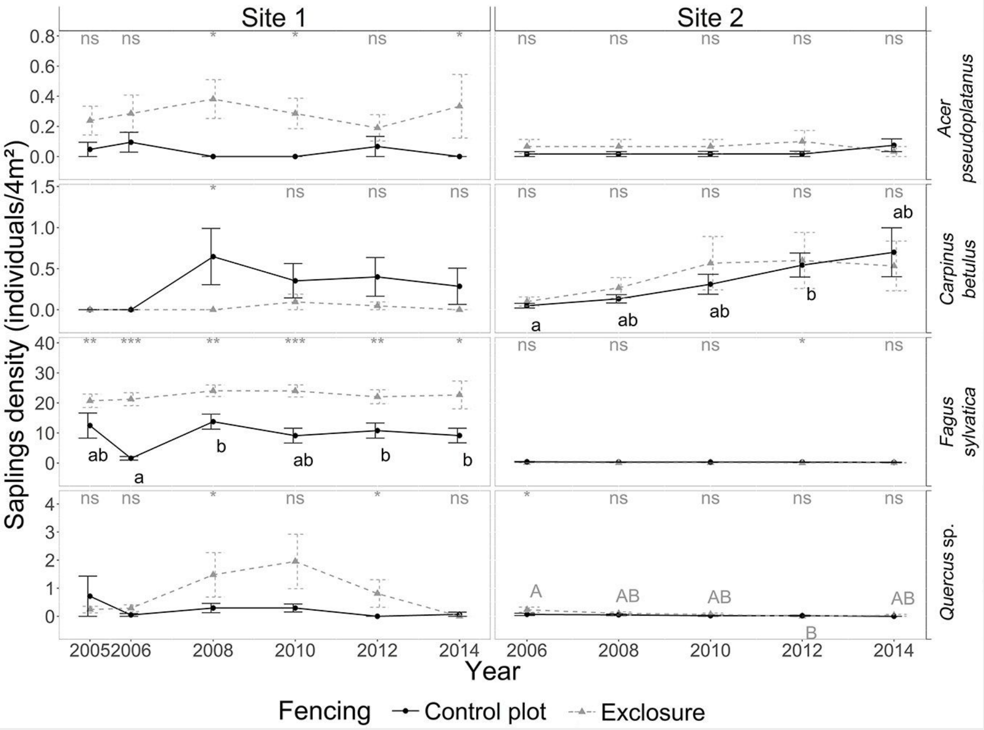
2006), but then progressively disappeared over time to reach 0% in 2014. Forbs dropped from 20% in 2005-2006, becoming completely absent by 2014 (Fig. 3). Bramble (*Rubus* spp.) showed the same general pattern, though the decrease was slightly delayed with maximum cover reached in 2008 (Fig. 3).

Site 2: Rubus-dominated understory

The exclusion of deer at site 2 did not result in an increase in cover for any of the four target tree species (Fig. 3). At site 2, tree recruitment was low (even negligible from a silvicultural point of view) throughout the study period for all four target species. Beech and oak seedlings and saplings were virtually absent. Hornbeam (and to a lesser extent sycamore maple) seedlings and saplings were present in significant numbers during the first field campaign in 2006, but in spite of this, their densities had already dropped to near-zero values by the following field campaign in 2008. Densities for these two species then remained low throughout the remainder of the study period (Fig. 4). Sapling height did not significantly differ between control and exclosure plots for any of the target tree species, although sycamore maple and hornbeam saplings tended to be taller in the exclosure than in the control plot (Fig. 6).

At site 2, bramble was the most frequent and abundant type of vegetation in the understory; it occurred in almost all the exclosure subplots at a mean cover of about 64.3 ± 2.3% overall. After fencing, bramble cover increased consistently from 43.8 ±

Fig. 5 - Yearly dynamics in sapling density (number of saplings per 4 m²) for the four target tree species in the presence of deer (control plot, dotted line) and in the absence of deer (exclosure plot, solid line) for sites 1 and 2 from 2005 to 2014. Note the different scales on the y-axes. For details on the legend, see Fig. 1.



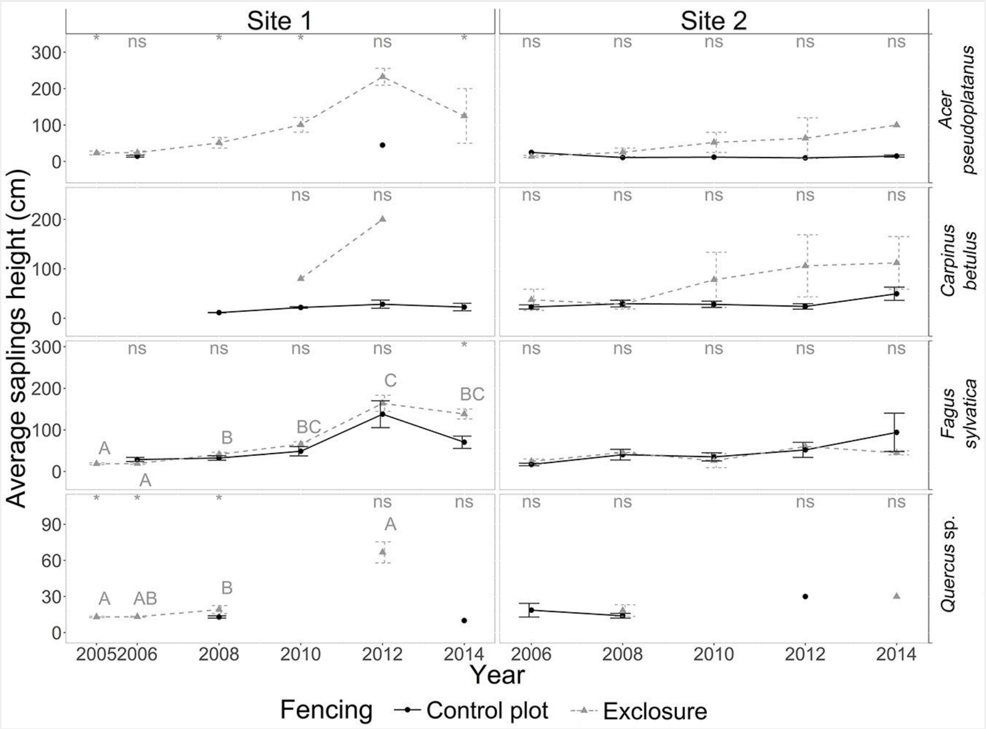


Fig. 6 - Yearly dynamics in the average height (cm) of saplings (15 cm < saplings > 3m) for the four target tree species in the presence of deer (control plot, dotted line) and in their absence (exclosure plot, solid line) for sites 1 and 2 from 2005 to 2014. Note the different scales on the y axes. For details on the legend, see Fig. 1.

4.7 % in 2005 to 65.8 ± 5.1% in 2014 in the exclosure plot (Fig. 3), while bramble cover remained stable (at about 18 %) throughout the study period in the control plot. Two plant species disappeared in the exclosure plot over time: raspberry decreased from about 18.3 ± 3.9 % cover in 2006 to 0.1 ± 0.1% in 2014; and *Carex remota* from about 17.4 ± 3.0 % in 2006 to 0.2 ± 0.1 % in 2014. Forb cover was consistently low in the exclosure and in the control plot (Fig. 3), while the abundant cover of graminoids and ferns dropped dramatically during the first two to six years, and switched from being more abundant to less abundant in the exclosure plot compared to the control plot.

Discussion

We observed that fencing consistently favored beech at site 1. These results are consistent with other studies on the effect of protection from browsing on tree recruitment: browsing reduced the sapling height of beech (Olesen & Madsen 2008) and other species both under a mature canopy (Stroh et al. 2008) and in clearcuts (Bergquist et al. 2009). Leonardsson et al. (2015) showed that, after ten growing seasons, exclosures favored oak regeneration by reducing ungulate browsing: some oak saplings reached a height of more than 130 cm in exclosures, but never in the presence of deer. However, in our case, fencing was not sufficient to assure the regeneration of tree species other than beech. It is therefore likely that excluding deer in our study favored the pre-existing beech seedlings (advanced regeneration).

We observed that fencing favored the rapid regrowth of bramble at site 2, where it became hyper-dominant in the exclosure plot within two years of fencing. The role of deer in controlling bramble and ground cover growth is consistent with the results by Kirby (2001); excluding deer can bring about explosive growth in bramble thickets (Kuiters & Slim 2002). Balandier and colleagues (2013) have shown that bramble is more adapted to shady environments and to disturbance (tolerant/resistant to browsing) than was first thought.

Concomitantly with the increase in beech and bramble cover, many herbaceous species disappeared and the cover of forbs, graminoids and ferns declined at both sites. Graminoids and ferns, therefore, benefitted from browsing pressure, a result which has also been found in other studies (Rooney 2001, Hegland et al. 2013). Likewise, the competitive ability of beech saplings was detrimental to plant community richness and diversity at site 1 in agreement with the results of other studies (Boulanger 2010).

Moreover, bramble is known to be a strong competitor for resource acquisition (Fotelli et al. 2001, Balandier et al. 2006, 2013). In agreement with Fotelli et al. (2002), Dodet et al. (2011) and Wasem & Häne (2008), we showed that under high bramble cover, the establishment, growth and survival of tree seedlings and saplings were weak. This is also consistent with a study performed by Harmer & Morgan (2007) on advanced oak. However, this contradicts the findings reported by Marquis (1981), who underlined that species like bramble, which reduce strongly competitive species like graminoids, ferns and forbs, can indirectly improve tree regeneration by reducing competition for resources. However, as shown by Bellingham et al. (2016), at lower deer densities, results should be more contrasted. Maintaining deer populations at relatively low levels should favor both community diversity and sapling growth.

Although diversity indices were calculated at the alpha-level and not at the gamma-level, we remain cautious about our results as they were possibly influenced by the differing number of subplots. Indeed, at site 1 the number of subplots was similar between the control and exclosure plots (n=21), but differed at site 2 (n=60 and 30 for the control and exclosure plot, respectively). Moreover, the number of subplots varied over time. This could account for some of the observed changes given that we did not account for this bias in the analyses other than by using a fixed subplot size and calculating the indices at the subplot level (alpha). Despite these caveats, our results are likely to be relatively robust since no clear spatial pattern was found using semi-variograms. We should also bear in mind that exclosure experiments inform about the recovery of a plant community after release from browsing and do not provide information about the community that would have occurred without the presence of deer (Mårell et al. 2012). Moreover, even though eight years may be considered rather short for a forest study, this time span should be long enough to observe the first responses of the forest understory to deer browsing pressure and is similar to time spans in other exclosure studies on oak (Leonardsson et al. 2015).

Furthermore, caution should be taken when interpreting our results as differences in stand and site characteristics were considerable. The lower basal area at the beginning of our experiment in the exclosure plot for site 2 ($p < 0.05$) could lead to a misinterpretation of our results. The higher shrub and herbaceous plant cover in the exclosure compared to the control could have been due to differences in light availability. However, we assumed that light availability at ground level was similar in the control and exclosure plots as Ellenberg's ecological indicator values (weighted by the relative cover) for light (modified by Julve 1998) showed no differences at the beginning of the experiment (see Fig. S2 in Supplementary material). Furthermore, differences were observed between control and exclosure plots after the first year of the experiment (cover percentage, number of saplings, etc.). This could have resulted from unobserved differences in the plots at the set-up of the experiment or from a rapid response of very dynamic species such as bramble to thinning events before our first measurements.

Thanks to these two concomitant eight-year experiments, we showed that fencing could be a useful tool to improve beech regeneration and growth. However, in our case, fencing combined with initial thinning was not sufficient to assure the regeneration of the other target tree species after eight years of deer exclusion; hence we are not able to offer guidelines to the forest manager who wishes to direct wood production towards tree species other than beech (in particular oak). Furthermore, removing deer browsing by fencing was not enough to favor tree recruitment at site 2, where bramble was widely present before the exclosure, and whose subsequent explosion suppressed other herbaceous understory species. However, a pattern does seem to emerge from these two case studies: shade-tolerant, browsing-tolerant, opportunistic species with a "sit and wait" strategy appear to dominate the community in the exclosure (beech in site 1 and bramble in site 2). Future management practices should no longer consider understory competition and deer browsing as two independent problems, nor should fencing be seen as a universal tool to mitigate deer impact on tree recruitment. Forest managers should pay particular attention to the presence of strong plant competitors and adapt their management accordingly.

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References

Apollonio M, Andersen R, Putman R (2010). European ungulates and their management in the 21st century. Cambridge University Press, New York, USA, pp. 604. [online] URL: http://books.google.com/books?id=-ycg5PtQPugC

Balandier P, Collet C, Miller JH, Reynolds E, Zedaker SM (2006). Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighbouring vegetation. Forestry 79: 3-27. - doi: 10.1093/forestry/cpi056

Balandier P, Marquier A, Casella E, Kiewitt A, Coll L, Wehrlen L, Harmer R (2013). Architecture, cover and light interception by bramble (*Rubus fruticosus*): a common understorey weed in temperate forests. Forestry 86: 39-46. - doi: 10.1093/forestry/cps066

Bellingham PJ, Richardson SJ, Mason NWH, Veltman CJ, Allen RB, Allen WJ, Barker RJ, Forsyth DM, Nicol SJ, Ramsey DSL (2016). Introduced deer at low densities do not inhibit the regeneration of a dominant tree. Forest Ecology and Management 364: 70-76. - doi: 10.1016/j.foreco.2015.12.013

Bergquist J, Löf M, Orlander G (2009). Effects of roe deer browsing and site preparation on performance of planted broadleaved and conifer seedlings when using temporary fences. Scandinavian Journal of Forest Research 24: 308-317. - doi: 10.1080/02827580903117420

Bertin S, Palmroth S, Kim HS, Perks MP, Mencuccini M, Oren R (2011). Modelling understorey light for seedling regeneration in continuous cover forestry canopies. Forestry 84: 397-409. - doi: 10.1093/forestry/cpr026

Boulanger V (2010). Pression d'herbivorie et dynamique des communautés végétales: influence à court et moyen termes des populations de cervidés sur la diversité des communautés végétales en forêt [Herbivory pressure and dynamics of plant communities: short- and medium-term influence of cervid populations on the diversity of plant communities in forests]. PhD thesis, Nancy - Henri Poincaré, France, pp. 289. [in French]

Braun-Blanquet J (1932). Plant sociology. The study of plant communities. McGraw-Hill Book Co. Inc., New York and London, pp. 476.

Davis MA, Wrage KJ, Reich PB, Tjoelker MG, Schaeffer T, Muermann C (1999). Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. Plant Ecology 145: 341-350. - doi: 10.1023/A:1009802211896

Dodet M, Collet C, Frochot H, Wehrlen L (2011). Tree regeneration and plant species diversity responses to vegetation control following a major windthrow in mixed broadleaved stands. European Journal of Forest Research 130 (1): 41-53. - doi: 10.1007/s10342-010-0406-z

Dumont B, Renaud PC, Morellet N, Mallet C, Anglard F, Verheyden-Tixier H (2005). Seasonal variations of red deer selectivity on a mixed forest edge. Animal Research 54: 369-381. - doi: 10.1051/animres:2005030

Dunn OJ (1964). Multiple comparisons using rank sums. Technometrics 6: 241-252. - doi: 10.1080/00401706.1964.10490181

Fischer HS (2015). On the combination of species cover values from different vegetation layers. Applied Vegetation Science 18: 169-170. - doi: 10.1111/avsc.12130

Fotelli MN, Geler A, Peuke AD, Rennenberg H (2001). Drought affects the competitive interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*: responses of growth, water status and δ^{13}C composition. New Phytologist 151: 427-435. - doi: 10.1046/j.1469-8137.2001.00186.x

Fotelli MN, Rennenberg H, Geler A (2002). Effects of drought on the competitive interference of an early successional species (*Rubus fruticosus*) on *Fagus sylvatica* L. seedlings: ^{15}N uptake and partitioning, responses of amino acids and other N compounds. Plant Biology 4: 311-320. - doi: 10.1055/s-2002-32334

Garel M, Bonenfant C, Hamann J-L, Klein F, Gaillard JM (2010). Are abundance indices derived from spotlight counts reliable to monitor red deer *Cervus elaphus* populations? Wildlife Biology 16: 77-84. - doi: 10.2981/09-022

Gill RMA, Beardall V (2001). The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74: 209-218. - doi: 10.1093/forestry/74.3.209

Greenberg CH, Smith LM, Levey DJ (2001). Fruit fate, seed germination and growth of an invasive vine-an experimental test of "sit and wait" strategy. Biological Invasions 3: 363-372. - doi: 10.1023/A:1015857721486

Harmer R, Morgan G (2007). Development of *Quercus robur* advance regeneration following canopy reduction in an oak woodland. Forestry 80: 137-149. - doi: 10.1093/forestry/cpm006

Hegland SJ, Lilleeng MS, Moe SR (2013). Old-growth forest floor richness increases with red deer herbivory intensity. Forest Ecology and Management 310: 267-274. - doi: 10.1016/j.foreco.2013.08.031

Hurlbert SH (1984). Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211. - doi: 10.2307/1942661

Julve P (1998). Baseflor. Index botanique, écologique et chorologique de la flore de France [Baseflor. Botanical, ecological and chorological index of the flora of France]. Web site. [in French] [online] URL: http://perso.wanadoo.fr/philippe.julve/catminat.htm

Kirby KJ (2001). The impact of deer on the ground flora of British broadleaved woodland. Forestry 74: 219-229. - doi: 10.1093/forestry/74.3.219

Kuiters AT, Slim PA (2002). Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biological Conservation 105: 65-74. - doi: 10.1016/S0006-3207(01)00204-X

Leonardsson J, Lof M, Gotmark F (2015). Exclosures can favour natural regeneration of oak after conservation-oriented thinning in mixed forests in Sweden: a 10-year study. Forest Ecology and Management 354: 1-9. - doi: 10.1016/j.foreco.2015.07.004

Mårell A, Ballon P, Hamard JP, Boulanger V (2012). Les dispositifs de type enclos-exclos: des outils au service de la gestion et de la recherche [Enclosure-exclosure: tools for management and research]. Revue Forestière Française 64: 139-150. [in French] [online] URL:

http://hal.archives-ouvertes.fr/hal-00758126/

Marquis DA (1981). Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. Research Paper NE-475, USDA Forest Service, Washington, USA, pp. 10. [online] URL: http://www.fs.fed.us/ne/newtown_square/publications/research_papers/pdfs/scanned/OCR/ne_rp475.pdf

Moser B, Schütz M, Hindenlang KE (2006). Importance of alternative food resources for browsing by roe deer on deciduous trees: the role of food availability and species quality. Forest Ecology and Management 226: 248-255. - doi: 10.1016/j.foreco.2006.01.045

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2016). "vegan": community Ecology Package. R package version 2: 3-3, web site. [online] URL: http://CRAN.R-project.org/package=vegan

Olesen CR, Madsen P (2008). The impact of roe deer (*Capreolus capreolus*), seedbed, light and seed fall on natural beech (*Fagus sylvatica*) regeneration. Forest Ecology and Management 255: 3962-3972. - doi: 10.1016/j.foreco.2008.03.050

Pielou EC (1966). The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144. - doi: 10.1016/0022-5193(66)90013-0

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

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [online] URL: http://www.r-project.org/

Rooney TP (2001). Deer impacts on forest ecosystems: a North American perspective. Forestry 74: 201-208. - doi: 10.1093/forestry/74.3.201

Schütz J (1999). Close-to-nature silviculture: is this concept compatible with species diversity? Forestry 72: 359-366. - doi: 10.1093/forestry/72.4.359

Stroh N, Baltzinger C, Martin JL (2008). Deer prevent western redcedar (*Thuya plicata*) regeneration in old-growth forests of Haida Gwaii: is there a potential for recovery? Forest Ecology and Management 255: 3973-3979. - doi: 10.1016/j.foreco.2008.03.039

Vincent JP, Gaillard JM, Bideau E (1991). Kilometric index as biological indicator for monitoring forest roe deer populations. Acta Theriologica 36: 315-328. - doi: 10.4098/AT.arch.91-33

Wasem U, Häne K (2008). Souris, chevreuils et ronces influencent les chênes pédonculés régénérés naturellement [Mice, deer and brambles influence the naturally regenerated pedunculate oak]. Forêt Entreprise 61: 8-10. [in French]

Supplementary Material

Tab. S1 - Summary table of herbaceous species presence/ abundance according to site and herbivory modality.

Fig. S1 - Evolution of plant community.

Fig. S2 - Julve plant community light index.

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