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

En Écologie-Biodiversité

École doctorale Gaia

Unité de recherche AMAP

Revisiter le rôle de la variabilité intraspécifique dans la coexistence des espèces : approches par modélisation et enseignements tirés des données forestières

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Revisiting the role of intraspecific variability in species coexistence: modelling approaches and insights from forest data

Présentée par Camille GIRARD-TERCIEUX
Le 16 décembre 2022

Sous la direction de Raphaël PÉLISSIER

Devant le jury composé de

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Acknowledgments

English version

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Version française (et plus personnelle)

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Sur une note très personnelle, j'aimerais maintenant faire un commentaire plutôt politique de mon expérience en thèse. Une thèse, c'est connu, est une épreuve. Dans toute épreuve, il y a du bon et du mauvais. Commençons par le bon. La recherche offre des choses merveilleuses. Travailler sur des sujets passionnants, sans avoir d'objectifs de rentabilité derrière (pour la recherche publique fondamentale tout du moins), voire même sans application directe (c'est mon cas, avec un sujet très théorique). Rencontrer des personnes du monde entier, avoir des conversations intellectuellement stimulantes, apprendre chaque jour. En écologie, découvrir des écosystèmes merveilleux, dans mon cas la forêt amazonienne – quel privilège. Bénéficier de grandes libertés sur les horaires, le code vestimentaire, la manière de travailler. Poursuivons avec le moins bon. Tout n'est pas inévitable, et j'espère que des améliorations verront le jour. En France, la recherche est encore majoritairement publique. Cependant, entre la réduction des budgets et une idéologie libérale notamment inspirée du système anglo-saxon, de plus en plus de financements sont privés ou en « partenariat public-privé », ce qui introduit des intérêts privés dans un domaine qui d'après moi devrait être complètement libre et indépendant. Le système de publication dépend d'éditeurs privés qui exploitent les scientifiques et freinent la diffusion du savoir. Il est de plus en plus difficile d'obtenir un poste fixe, et les chercheuses et chercheurs, ayant pourtant prouvé leur vaillance académique avec huit années d'études et plusieurs années d'expérience en recherche, doivent bien souvent enchaîner les contrats précaires, notamment en faisant fonctionner l'Université mais sans la rémunération ni le statut qui devraient en découler. Cette situation met les individus en compétition pour les postes, avec une course à la publication qui nuit à la qualité de la recherche, et crée une pression et une précarité qui en font fuir beaucoup, au premier rang desquels des profils qui supportent mal la pression ou ont besoin de sécuriser leur situation financière et de s'installer. Les profils les plus « sensibles » ou « empathiques » de la recherche sont ainsi écartés, alors qu'ils auraient tant à apporter au vu de ce qui s'y passe. En particulier, cela fait fuir beaucoup de jeunes femmes qui n'ont pas été éduquées à avoir une attitude combative et à s'épanouir dans la compétition, et ont pour certaines des projets de vie incompatibles avec la longue période de précarité qui leur est promise dans une carrière de chercheuse. De plus, la pression à la publication, à la « réussite » et à l'« excellence » fait des ravages psychologiques, comme en témoignent les chiffres de la dépression et de l'anxiété parmi les doctorant·e·s. Ma propre expérience corrobore ces chiffres. J'ai eu besoin d'une psychothérapie et de médicaments pour gérer mon anxiété grandissante et j'ai été au bord du burn-out malgré une équipe qui me soutenait - car la pression est systémique. Nombre de mes camarades ont besoin de psychothérapie et de soutien chimique. Nous n'en parlons pas car c'est tabou, dans la recherche comme ailleurs. Nous nous sentons toutes et tous comme des imposteurs qui ne méritent pas leur financement et ne seront jamais assez bons, car nous savons que nous devrons toujours prouver notre valeur, nous comparer aux autres. Certain·e·s souffrent en plus d'un travail solitaire (alors que la recherche se fait en équipe), souvent lié à un encadrement de piètre qualité, ce qui n'est pas mon cas. Cette mise sous pression des étudiant·e·s et jeunes chercheuses et chercheurs peut aussi créer des situations de dépendance envers la hiérarchie, ce qui dans certains cas mène à des abus qui vont du harcèlement professionnel aux agressions sexuelles en passant par des situations d'emprises, comme dénoncé dans le livre d'Adèle B. Combes, « Comment l'Université broie les jeunes chercheurs » ou encore dans la tribune de 2021 dénonçant la situation à Barro Colorado Island, prestigieux site de recherche en écologie tropicale au Panama. Si je n'ai pas subi de torts de la sorte, je connais autour de moi de nombreux cas d'abus, et cela crée un sentiment de vulnérabilité et d'injustice peu propices à l'épanouissement professionnel. Je pense que la recherche compte assez de cerveaux fonctionnels pour mettre au point des moyens efficaces pour se transformer en un milieu respectueux où le bien-être au travail est de mise. Encore faut-il en avoir la volonté politique, car il faut les moyens de ses ambitions. Encore faut-il également que les jeunes chercheuses et chercheurs aient une voix et n'aient pas peur des conséquences pour leur carrière. À titre d'exemple, il n'y a pas de syndicat spécialisé pour les doctorant·e·s, et la peur de passer pour une personne feignante ou « trop sensible » en empêchent beaucoup d'exprimer leur mal-être. Encore faut-il aussi que les chercheuses et chercheurs en poste permanent soutiennent celles et ceux qui n'ont pas de poste permanent, par exemple en se mobilisant massivement lors des appels à la grève ou à la manifestation. Or j'ai observé un immobilisme sur fond de surmenage, alors même que l'avenir de la recherche publique est incertain. Un travail doit aussi se faire en amont du doctorat, car en tant que doctorant·e·s nous sommes les produits de tout un système éducatif qui explique en partie que nous vivions mal notre expérience de jeunes chercheuses et chercheurs. J'espère pour finir qu'à l'avenir, celles et ceux qui ont pour mission d'approfondir et de transmettre la connaissance humaine, oseront se positionner pour le progrès social, dans leur branche et même plus loin.

Résumé en français

Contexte

Le nombre d'espèces coexistant dans une communauté au sein d'un même niveau trophique fascine depuis des millénaires et se trouve à l'origine de questions centrales en écologie scientifique. En effet, comment expliquer que des centaines d'espèces qui requièrent les mêmes ressources et devraient donc être en compétition, coexistent sur le long terme, comme les espèces d'arbres dans une forêt, de coraux dans un récif ou encore de bactéries dans le microbiote intestinal ? (Hutchinson 1961). Ce paradoxe est le sujet d'un domaine entier de l'écologie, la théorie de la coexistence. Plusieurs mécanismes ont été proposés (Chesson 2000a), qui peuvent être classés en deux grandes théories. La première, la théorie de la niche écologique, fait l'hypothèse que ce sont les différences entre espèces qui leur permettent de coexister, par exemple en utilisant plus ou moins efficacement les différentes ressources ou en ayant des besoins très légèrement différents les unes des autres (Gause 1934; Hutchinson 1957). La deuxième, la théorie neutre, fait l'hypothèse que les différences qu'on observe entre les espèces ne jouent en fait pas sur leur capacité à coexister, mais que seuls des processus aléatoires déterminent la coexistence des espèces : mortalité et recrutement stochastiques, spéciation, immigration (Hubbell 2001). Cependant, la majorité des mécanismes proposés ont été testés en utilisant des attributs (par exemple des paramètres démographiques et des traits fonctionnels) moyens par espèce. Ces dernières décennies, cette approche a été remise en question car la variabilité intraspécifique - les différences observées au sein des espèces - a été remise sur le devant de la scène, avec des études montrant que son ampleur était loin d'être négligeable au sein des communautés (Violle et al. 2012). On estime par exemple dans une méta-analyse que la variabilité intraspécifique représente un quart de la variabilité totale au sein d'une communauté (Siefert et al. 2015). Dans le sillon de ces études quantifiant la part de variabilité au sein des espèces, la question de ses conséquences écologiques s'est posée. Et en particulier, la question de son rôle dans la coexistence des espèces. Là encore, deux hypothèses principales ont été proposées, découlant des deux manières d'appréhender la coexistence des espèces. La première, basée sur la théorie de la niche, suppose que la variabilité intraspécifique entraîne une superposition des niches écologiques des espèces, menant à une exclusion compétitive accrue (MacArthur and Levins 1967). La seconde, plutôt basée sur la théorie neutre, suppose que la variabilité intraspécifique permet à des espèces en moyenne peu performantes de se maintenir grâce à l'émergence d'individus plus performants (Vieilledent et al. 2010). Dans les deux cas, la représentation de la variabilité intraspécifique est semblable : elle est considérée comme un bruit qui brouille les différences entre les espèces (Lichstein et al. 2007; Hart et al. 2016). Cette vision se retrouve dans les modèles théoriques qui cherchent à explorer le rôle de la variabilité intraspécifique dans la coexistence des espèces : dans la majorité des cas, celle-ci est modélisée à l'aide de tirages aléatoires indépendants, et n'a donc pas de structure dans le temps et dans l'espace (Hart et al. 2016; Lichstein et al. 2007; Courbaud et al. 2012). Cependant, cette manière d'introduire la variabilité intraspécifique est une hypothèse forte qui est rarement explicitée et dont les conséquences ne sont pas testées. En effet, la variabilité intraspécifique, qu'elle provienne de réponses à des stimuli environnementaux ou de différences génétiques, peut être structurée dans le temps et dans l'espace et ne serait donc pas implémentée de manière réaliste dans les modèles de dynamique des communautés.

Objectifs

L'objectif principal de cette thèse est de fournir des éléments de réflexion sur la nature, la structure, et la manière dont la variabilité intraspécifique est considérée en écologie, en particulier dans les modèles de dynamique des communautés. Plus précisément, il s'agit de montrer que la variabilité intraspécifique est plus qu'un simple bruit qui brouillerait les différences entre espèces. En effet, c'est cette vision qui prédomine, en particulier dans les études de modélisation, dans lesquelles la variabilité intraspécifique est souvent représentée par des tirages aléatoires indépendants dans une distribution de probabilité, mais sans discussion explicite de la signification et des implications de cette hypothèse. Plusieurs sous-objectifs structurent la thèse. Premièrement, montrer de manière pédagogique que la variabilité intraspécifique peut émaner de variations environnementales dans de nombreuses dimensions qui ont été imparfaitement décrites, et pas nécessairement de variations génétiques entre individus d'une même espèces (Chapitre 1). Deuxièmement, montrer que la variabilité intraspécifique possède une structure dans le temps et dans l'espace, qui n'est donc pas bien prise en compte dans les modèles de dynamique des communautés, et illustrer comment la structure de l'environnement peut être à l'origine de cette structure (Chapitre 1). Troisièmement, montrer que la manière d'introduire la variabilité intraspécifique dans les modèles de dynamique des communautés a des conséquences sur la composition des communautés simulées, en particulier sur le nombre d'espèces qui coexistent (Chapitre 2). Quatrièmement, proposer un modèle théorique expliquant l'émergence d'une structure dans les corrélations des performances individuelles (phénomène observé dans les données de travaux préalables, Clark 2010) et permettant de maintenir la coexistence de nombreuses espèces via l'association de variations environnementales dans de nombreuses dimensions et du partitionnement de l'environnement par les différentes espèces (Chapitre 3). Et enfin, proposer une méthode de modélisation permettant d'introduire une covariance structurée sans connaissances sur l'origine de cette structure, ce qui permet de reproduire des motifs comme la coexistence des espèces dans le modèle, et constitue une piste pour les modèles de dynamique des communautés, notamment en permettant d'inclure les connaissances disponibles sur les variables environnementales (Chapitre 3). Nous espérons amener une réflexion sur la manière de considérer et de représenter la variabilité intraspécifique en écologie des communautés. Nous proposons notamment des perspectives pour l'amélioration de la connaissance de la structure de la variabilité intraspécifique et des causes de cette structure, ainsi que pour l'amélioration des modèles de dynamique des communautés.

Principaux résultats

Dans le Chapitre 1, un premier résultat consiste en l'illustration claire que la variabilité intraspécifique observée peut provenir de variations environnementales qui n'ont pas été prises en compte dans les analyses. Ce premier résultat est obtenu à l'aide d'une illustration théorique (et d'un modèle théorique de dynamique des communautés dans le Chapitre 2) et de la partition de variance de la croissance de clones d'Eucalyptus dans un design expérimental de common garden. En effet, dans ce dernier exemple, une part importante de la variabilité entre individus est due à des déterminants non-génétiques. Un second résultat montre que dans trois forêts tropicales contrastées, la variabilité intraspécifique de la croissance est structurée dans l'espace, et que malgré une forte variabilité intraspécifique observée, les individus d'une même espèce ont une croissance plus similaire que les individus d'espèces différentes. Ainsi, malgré une forte variabilité intraspécifique, les différences entre espèces ne sont pas effacées (Chapitre 1). De ces deux premiers résultats, on conclut que la représentation usuelle de la variabilité intraspécifique dans les modèles de dynamique des communautés, à savoir un bruit non structuré qui diminue les différences entre les espèces, ne semble pas bien refléter la réalité. On propose donc une expérience virtuelle pour le montrer.

Dans le Chapitre 2, un troisième résultat montre ainsi que la manière d'introduire la variabilité intraspécifique dans un modèle de dynamique des communautés a des conséquences sur les sorties du modèle, notamment en terme de nombre d'espèces finales et d'abondances relatives. Ce résultat a été obtenu en construisant une expérience virtuelle qui permet de comparer les simulations issues du même simulateur, mais avec différentes méthodes de calcul de la performance individuelle (avec une variabilité intraspécifique structurée ou non dans l'espace). On montre ainsi que les communautés finales obtenues avec une variabilité intraspécifique non-structurée ne sont pas réalistes, comparées à une situation de référence où la variabilité intraspécifique est issue de variations environnementales structurées dans l'espace. De plus, Les communautés simulées avec une variabilité intraspécifique non structurée ne sont pas plus réalistes (par rapport à la situation de référence), en comparaison à des communautés obtenues en ignorant complètement la variabilité intraspécifique, que dans les cas où très peu d'informations sur l'environnement sont connues. Ainsi, dans la majorité des cas, substituer la variabilité structurée issue de variations environnementales par une variabilité aléatoire non structurée n'est pas une méthode satisfaisante. En parallèle, améliorer les connaissances sur les déterminants de la structure de la variabilité intraspécifique (par exemple en mesurant plus de variables environnementales, à des échelles plus fines, ou en mesurant plus précisément les réponses des espèces) ne semble pas être une solution facilement déployable. Ce troisième résultat amène donc à la recherche d'une manière d'introduire la structure de la variabilité intraspécifique dans les modèles de dynamique des communautés.

Dans le Chapitre 3 final, un quatrième résultat consiste en l'explication de l'émergence d'une structure dans les corrélations des performances individuelles dans un modèle théorique, structure associée à la coexistence de nombreuses espèces. Plus précisément, on y montre que les différences entre espèces ne suffisent pas à obtenir une forte coexistence, mais que c'est le cas lorsque les espèces peuvent répondre - chacune un peu différemment - à des variations dans de nombreuses dimensions, par exemple la variation de variables environnementales comme la température. Dans ce modèle, comme dans celui du Chapitre 2, la coexistence est permise par la haute dimensionalité d'une part, et les différences entre espèces d'autre part, qui, ensemble, permettent le partitionnement de l'environnement par les espèces. Les différents niveaux de coexistence obtenus selon la dimensionalité sont associés à certaines configurations de la corrélation des performances individuelles entre et au sein des espèces : dans le cas où la haute dimensionalité rend la coexistence de nombreuses espèces possible, les corrélations entre individus d'une même espèce sont plus fortes que les corrélations entre individus d'espèces différentes. Un dernier résultat consiste en la mise au point d'une méthode permettant d'inclure dans des modèles de dynamique des communautés cette structure de la variabilité intraspécifique due à la réponse des espèces à des variations dans de nombreuses dimensions. Cela permet de maintenir la coexistence de nombreuses espèces malgré le manque de connaissances sur les déterminants de cette structure comme les variations environnementales et les réponses des espèces à ces variations. Un modèle hybride permet de plus d'inclure cette structure parallèlement aux connaissances disponibles sur les variables environnementales. Cette possibilité serait particulièrement utile en modélisation, notamment pour les modèles forestiers basés sur des données.

Discussion

Plusieurs axes de discussion sont proposés afin de replacer le travail présenté dans un contexte scientifique plus large, d'en dessiner certaines limites, et d'ouvrir des perspectives.

D'abord, les choix de modélisation et les approches scientifiques sont discutés, et les modèles proposés dans la thèse sont inscrits dans un cadre de modélisation plus large. En effet, les analyses de données effectuées dans le Chapitre 1 avaient pour objectif de détecter des tendances dans les données. Ainsi, ces analyses adoptent une appproche inductive, qui a tantôt été promue et critiquée en écologie (Wilson 2003). D'autre part, les analyses effectuées à l'aide de modèles et illustrations théoriques dans chacun des chapitres avaient pour objectif de tester une hypothèse et adoptent donc une approche déductive. Cependant, ces tests ne permettent pas de falsifier d'hypothèse suivant une démarche poppérienne, mais de vérifier les hypothèses émises. Bien que la falsification d'hypothèse soit la seule méthode considérée comme rigoureusement scientifique, elle est difficilement applicable en écologie (bien que ce ne soit pas impossible), et la vérification, qui permet tout de même d'accroître les connaissances scientifiques, est largement répandue en écologie scientifique (Wilson 2003). De plus, les modèles utilisés dans les Chapitre 2 et 3 sont positionnés dans un cadre conceptuel permettant de classer les modèles et théories en écologie selon trois axes, ce qui permet de replacer nos modèles par rapport à d'autres approches. Il en ressort que nos modèles reposent sur une structure simple où les comportements des individus sont déterminés par des paramètres fixés ; qu'ils ne mettent pas en place de rétro-action, ni entre espèces (avec par exemple dans le modèle du Chapitre 3 une densité-dépendance qui n'est pas spécifique à l'espèce), ni entre les individus et les variables environnementales ; et enfin, que leur dynamique est stationnaire puisqu'elle n'est pas impactée par des événements historiques majeurs (Barbier, en préparation).

Ensuite, la notion de haute dimensionalité, au cœur des mécanismes de coexistence des modèles proposés, est développée. En effet, il peut sembler irréaliste que la coexistence repose sur un très grand nombre de dimensions notamment dans le modèle du Chapitre 3, tandis qu'un faible nombre de ressources limitantes sont identifiées pour les plantes (lumière, eau et nutriments du sol). Cependant, de nombreuses autres dimensions de l'environnement peuvent jouer sur la performance des plantes, comme la température, la présence et la densité d'ennemis naturels ou la concentration en éléments toxiques dans le sol. De plus, la dimensionalité n'est pas uniquement celle de l'environnement, mais aussi celle de l'espace des réponses des espèces à ces variables environnementales. Or, la réponse des espèces à l'environnement est rarement linéaire. Une réponse non linéraire implique plusieurs paramètres pour décrire la réponse de l'espèce à un gradient environnemental, ce qui signifie qu'en réalité un unique axe environnemental peut consituter plusieurs dimensions. En parallèle, l'environnement variant dans le temps et l'espace, les conditions de coexistence exigées par les modèles des Chapitre 2 et 3 sont bien réunies.

Par la suite, une réflexion est menée sur l'importance de l'origine *vs.* la structure de la variabilité intraspécifique. Les deux origines principales de la variabilité intraspécifique (génétique et environnementale) ont des conséquences différentes, seule la première induisant des changements héritables sur de nombreuses générations et permettant donc l'évolution de l'espèce (Moran et al. 2016). Cependant, il est difficile de distinguer la source de la variabilité dans les données, en particulier dans les milieux naturels non expérimentaux. Dans cette thèse, la structure de la variabilité est mise en avant par rapport à son origine. En particulier, la solution proposée dans le Chapitre 3 pour inclure la structure de la variabilité intraspécifique ignore l'origine de cette structure. Cependant la démarche souvent adoptée par les écologues consistant à ignorer les effets de l'évolution est remise en cause. En effet, cette démarche s'appuie sur des pas de temps différents entre les interactions locales entre individus (comme la compétition et la facilitation) d'une part et l'évolution d'autre part. Or des observations montrent que ces pas de temps peuvent se superposer, et que les rétroactions éco-évolutives jouent un rôle non négligeable dans la dynamique des communautés (Bolnick et al. 2011a). Bien que cela soit hors du champ d'application de cette thèse, il est donc important d'inclure l'évolution dans les modèles de dynamique des communautés qui évaluent le rôle de la variabilité intraspécifique dans la coexistence des espèces.

Enfin, les relations entre corrélations, compétition et coexistence des espèces sont discutées. En effet, dans la thèse, un lien de causalité est supposé entre d'une part des corrélations plus fortes de la performance au sein qu'entre les espèces, d'autre part une compétition intraspécifique supérieure à la compétition interspécifique, et enfin la coexistence stable. Il n'est pas évident que l'observation de corrélations plus fortes de la performance au sein des espèces soit le signal d'une forte compétition intraspécifique. En effet, des congénères en forte compétition auraient au contraire des réponses négativement corrélées (si l'un grandit bien, il impacte négativement la croissance de l'autre). L'observation de corrélations plus fortes de la performance au sein des espèces pourrait en revanche indiquer que la dynamique est dominée par des facteurs environnementaux auxquels les individus ne font que répondre et qu'ils n'influent pas en retour. De plus, si le fait de considérer que la coexistence des espèces peut s'expliquer entièrement par leur compétition est issu d'une longue tradition en écologie, cela relève à la fois d'une hypothèse forte et d'une inscription - souvent internalisée - dans un contexte idéologique. Cette hypothèse est en effet issue d'une ambition de l'écologie de se rapprocher des sciences « dures » comme la physique, en formulant de grands principes généraux (Maris et al. 2018). Par ailleurs, l'idée que l'échelle individuelle et la compétition sont les éléments pertinents pour comprendre la dynamique des communautés, idée dans laquelle cette thèse s'inscrit, peut être comparée à une appréhension libérale du monde qui ne va pas de soi.

La thèse s'ouvre sur des perspectives concrètes en terme de tests dans les données et de pistes d'amélioration des modèles de dynamique des communautés. Il serait en effet intéressant d'examiner la structure spatiale et temporelle des réponses individuelles dans différents sites forestiers, dans différents biomes, et avec différents attributs (croissance individuelle mais aussi recrutement, mortalité, traits fonctionnels, *etc.*) et de relier cette structure aux variations environnementales, aux modes de dispersion des plantes, à la structure génétique, *etc.* Cela permettrait de mieux comprendre les origines et la structure de la variabilité intraspécifique. Par ailleurs, implémenter la structure de la variabilité intraspécifique dans les modèles de communauté serait utile pour améliorer les prédictions de ces modèles. Le modèle hybride présenté dans le Chapitre 3 pourrait être une manière efficace d'introduire cette structure sans connaissances supplémentaires sur ses déterminants. Obtenir des prédictions plus réalistes présente des applications directes, notamment pour projeter les conséquences du changement climatique sur la biodiversité dans différents scénarii, afin d'éclairer les décideurs.

Conclusion générale

Dans le contexte de l'énigme encore incomplètement résolue de la coexistence, la variabilité intraspécifique a été considérée comme une piste potentielle. Son effet sur la coexistence des espèces a donc été étudié, principalement à l'aide de modèles théoriques de dynamique des communautés qui ont mené à des résultats contradictoires. Dans ces modèles théoriques, la variabilité intraspécifique a été presque systématiquement introduite comme un bruit aléatoire qui rendait les espèces plus similaires. Dans cette thèse, nous avons exploré une autre vision de la grande variabilité intraspécifique observée dans les données, en suggérant qu'elle peut être la conséquence de réponses spécifiques des espèces à des variations environnementales dans de nombreuses dimensions mal caractérisées. Nous avons ainsi replacé la variabilité intraspécifique dans le cadre de la niche multidimentionnelle (et donc dans un contexte scientifique et philosophique particulier), où tant l'environnement que la réponse des espèces à celui-ci peuvent contribuer à la multidimentionnalité. Dans ce but, nous avons utilisé des approches complémentaires, allant de la simple illustration théorique à des analyses de données expérimentales clonales et de données d'inventaires forestiers, en passant par des expériences de simulation. Ce faisant, nous avons adopté des méthodes scientifiques inductives et déductives, et testé nos hypothèses par la vérification. En soulignant l'importance de la structure de la variabilité intraspécifique pour la coexistence et la dynamique des communautés, nous espérons déclencher une nouvelle façon de considérer et de représenter la variabilité intraspécifique observée en écologie des communautés. Les modèles présentés ici sont bien sûr faux - comme tout modèle - car ils reposent sur des hypothèses fortes, et ne prétendent en aucun cas représenter fidèlement la réalité. Cependant, ils sont utiles pour répondre (partiellement) aux questions que nous avons posées dans cette thèse : la structure de la variabilité intraspécifique peut-elle découler de la structure des variables environnementales qui n'ont pas été prises en compte ? Oui (Chapitre 1). La façon dont la variabilité intraspécifique est introduite dans un modèle de dynamique des communautés a-t-elle une importance pour la coexistence des espèces et la composition des communautés ? Oui (Chapitre 2). La structure de la variabilité intraspécifique observée dans les données par Clark (2010) peut-elle être expliquée simplement par les réponses des espèces aux variations environnementales ? Oui (Chapitre 3). Cela conduit-il à la coexistence ? Oui, mais ce lien doit être discuté (Chapitre 3 et Discussion générale). Cette structure de variabilité intraspécifique peut-elle à elle seule reproduire des caractéristiques dans les modèles telles que la richesse et la diversité des espèces, les rangs des espèces ou le filtrage environnemental dans un modèle de dynamique des communautés ? Oui, mais seulement en partie (Chapitre 3). En proposant des pistes d'amélioration pour l'intégration de la structure de la variabilité intraspécifique dans les modèles de dynamique des communautés, et notamment en proposant une méthode qui permet d'obtenir la coexistence des espèces sans paramètres précis et pouvant intégrer des données de terrain, nous offrons des perspectives concrètes pour l'écologie fondamentale et appliquée.

General introduction

I. Species coexistence in ecology

I.1. Observed species diversity in communities

The description of the diversity of life forms has long been an important subject for humankind. While our ancestors had great interest in understanding which organism could be eaten, taxonomy (words in teal are defined in the Glossary), although consistently related to human uses, has also been a source of scientific questioning (as well as artistic interest *e.g.* in naturalist drawing, Figure 1). While the first recorded attempts to describe and classify life date back to 3000 BC in ancient China and 1500 BC in Ancient Egypt (Manktelow 2010), in the western world, Aristotle (384–322 BC) and his pupil Theophrastus (370–285 BC) are recognised as the first to describe several hundreds of plants and animals, followed by the roman Plinus the elderly, the Greek Pedanius Dioscorides and many others throughout the centuries (*e.g.* Conrad Gessner's *Historia animalium*, Ulisse Aldrovandi's *Teatro della natura* and *Ornithologiae*). The Linnean classification (in *Species plantarum* and *Systema Naturae*) was the first that brought the principles of our modern ways to name species, with a binary nomenclature (Genus and species names, *e.g.* *Crataegus monogyna*). Nowadays, the definition of species is continuously informed by phylogeny (species' family tree) and genetics alongside the more classical morphological (visual) and ecological (behaviour, regime, habitat, interactions with other species) description, and arises scientific as well as philosophical questions (Wiley 1978; Hey 2001).

One of the most remarkable features of the natural world is the diversity of forms and functions that can coexist in a single community at the same trophic level, for instance in some communities of microorganisms (phytoplankton, gut bacteria) or more famously in coral reefs and tropical forests (Figure 2). To give an order of magnitude, a tropical forest can shelter up to 900 plant species in a single hectare (100×100 m) (Wilson et al. 2012). While a central question in ecology and evolution is the origin of this biodiversity (*e.g.* Eiserhardt et al. 2017), coexistence theory focuses on asking how so many species can coexist at a given instant, in a given community.

I.2. Coexistence theory

Among the many species that are observed within a community, some of them have the same requirements to survive: they all "eat" the same thing (interview of Peter Grubb, 2015). This is the case for plants, which all need light, water, carbon dioxide and soil nutrients to perform photosynthesis, which is the way they transform solar energy into chemical, carbon-based energy (Farquhar et al. 1980), enabling them to go through their life cycle. However, dozens (*e.g.* in temperate forests like the Rambouillet forest near Paris) to hundreds (*e.g.* in tropical forests like the Nouragues nature reserve in French Guiana) of tree species coexist within a single hectare. Coexistence theory is the branch of ecology that was developed around the paradox of how species are able to coexist while competing for the same resources (Hutchinson 1961). This paradox was first formulated for phytoplankton communities, and was therefore historically called "the Plankton paradox", but was soon generalised to other communities and called the "biodiversity" or "coex-

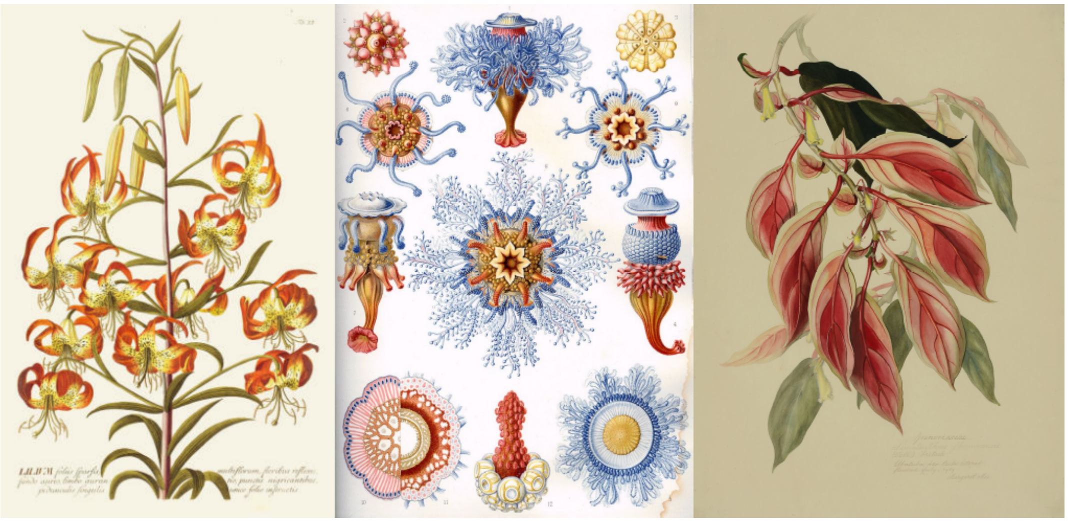

Figure 1: Examples of scientific drawings Scientific drawings have the important scientific role to represent observations accurately, but their aestheticism is to be noted. From left to right: Georg Dionysius Ehret - *Lilium superbum*, LILIUM, TAB. XI, PUB. 1750-1773 in *Plantae selectae*. Ernst Haeckel - Kunstformen der Natur (1904), plate 17: Siphonophorae. Margaret Mee - *Gesneriaceae*, *Nematanthus fluminensis (vell.) Fritsch*, Ubatuba, São Paulo litoral, flowered July, 1959.

istence paradox". Several concepts, frameworks and hypotheses have been proposed to approach coexistence theory and to solve this paradox using various approaches (Chesson 2000b; Wright 2002; Wilson et al. 2019, Figure 4a and c), like theoretical development and modelling (*e.g.* Lotka 1925; Volterra 1926; Hutchinson 1957; Tilman 1982; Hubbell 2001; Levine and HilleRisLambers 2009), data-analysis (*e.g.* Janzen 1970; Connell 1971; Grubb 1977; Hubbell 1999; Clark 2010; Barbier et al. 2021) and experiments (*e.g.* Grubb 1977; Tilman 1982; Levine and HilleRisLambers 2009; Livingston et al. 2012; Bagchi et al. 2014).

The question of how species coexist is an intellectual puzzle, but is also crucial for the protection of biodiversity. Biodiversity supports ecological services (also called Nature's contribution to people) like water filtration, soil fertility, pollination or even global climate regulation (Millennium Ecosystem Assessment 2005; IPBES 2019, Figure 5). This question is thus also a challenge for humankind as the dramatic, anthropogenic erosion of biodiversity that is currently accelerating, puts ecosystems as well as human societies under threat. In this context, better understanding how biodiversity arises and is maintained is the first step to protect it (Cordonnier et al. 2018). Understanding the mechanism of community assembly (*i.e.* of species coexistence) is also crucial because depending on these mechanisms, the biodiversity-ecosystem functioning (BEF) relationships can change (Crawford et al. 2021), with consequences on ecological services and feedbacks between biodiversity and function loss (Loreau et al. 2001; Naeem et al. 2012). Understanding why species disappear (*i.e.* mechanisms of community "disassembly") is crucial as well, because it also impacts ecosystem functioning (*e.g.* García-Valdés et al. 2018). Overall, coexistence theory is one of the keystones of ecology and is therefore related to many sub-fields of ecology, including concrete applications.

I.2.a. The niche theory

Ecological niche and competitive exclusion principle The naturalist observation and description of species, of their habitat, behaviour, relationships with other species, diet, *etc.*, as well

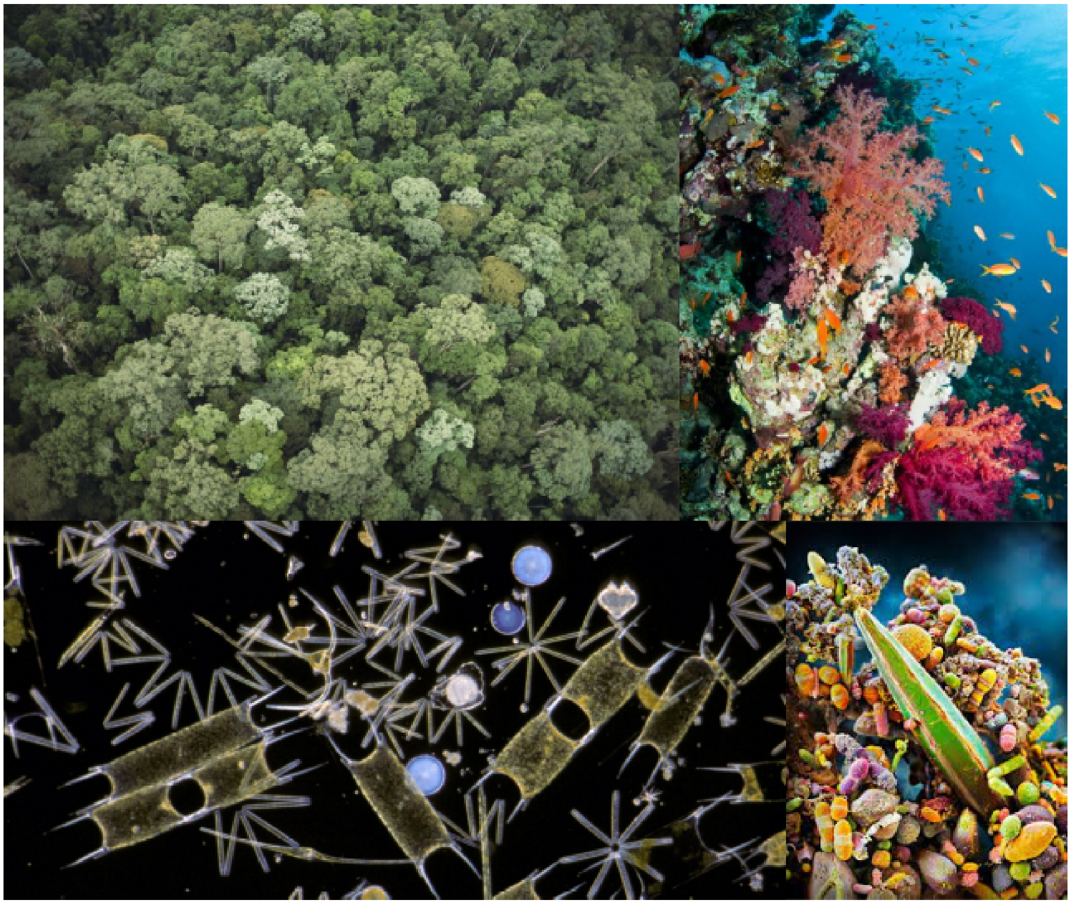

Figure 2: Some examples of hyperdiverse communities as presented in media The great diversity of these communities are a scientific subject, but also a source of curiosity for a larger audience. All images were found on the National Geographic journal's website. From up left to bottom right: Borneo's rainforest forest; Photograph by J. P. Blair, National Geographic. Jackson Reef in the Red Sea; Photograph by P. Colley, MyShot. Phytoplankton; Photograph by D.P. Wilson, Minden Pictures. Microscopic observation of human faeces; Photograph by M. Oeggerli, NatGeo Image Collection.

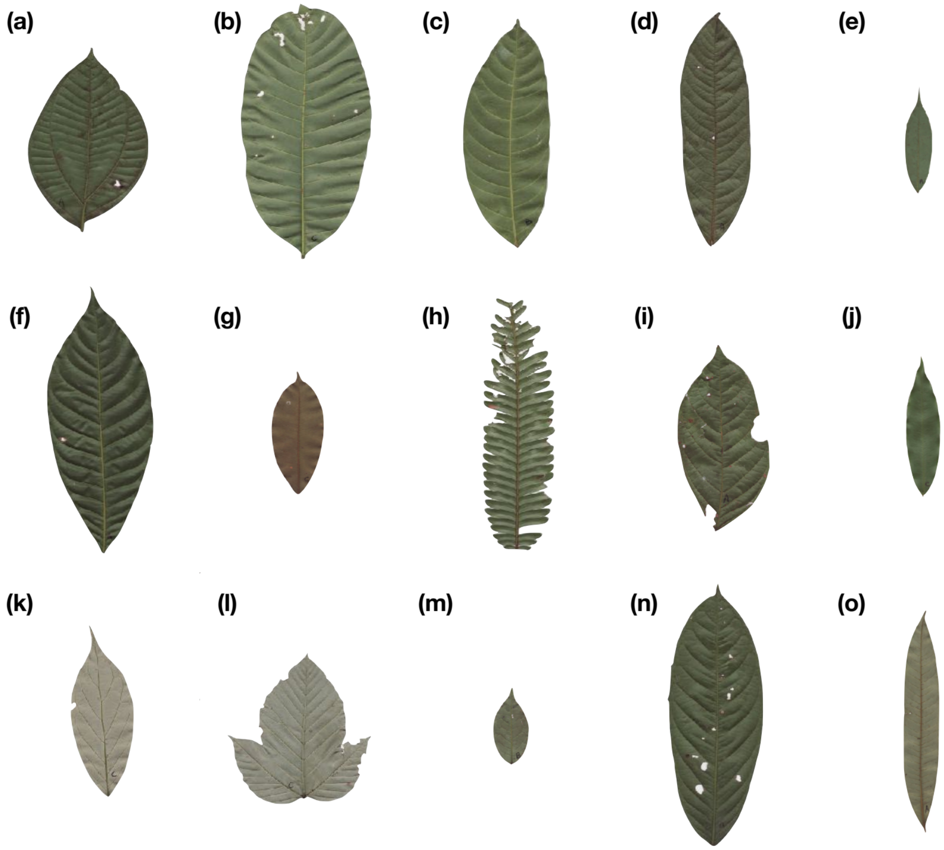

Figure 3: Interspecific differences in leaf aspects in a single community. Leaf forms, sizes, colours and veination vary greatly across species, illustrating functional differences across them. Here all leaves were sampled in the same terra firme plot in French Guiana and the species belong to various families: (a) *Bellucia grossularioides* (Melastomataceae); (b) *Macoubea guianensis* (Apocynaceae); (c) *Tabernaemontana undulata* (Apocynaceae); (d) *Fusaea longifolia* (Annonaceae); (e) *Xylopia benthamii* (Annonaceae); (f) *Pouteria aubrevillei* (Sapotaceae); (g) *Micropholis guyanensis* (Sapotaceae); (h) *Parkia decussata* (Fabaceae); (i) *Inga pezizifera* (Fabaceae); (j) *Ouratea leprieuri* (Ochnaceae); (k) *Licania micrantha* (Chrysobalanaceae); (l) *Siparuna poeppigii* (Siparunaceae); (m) *Diospyros capreifolia* (Ebenaceae); (n) *Eschweilera grandiflora* (Lecythidaceae); (o) *Protium cuneatumn* (Burseraceae). For compound leaves, only a leaflet is shown, and large leaves could not be shown. Copyright Claire Fortunel.

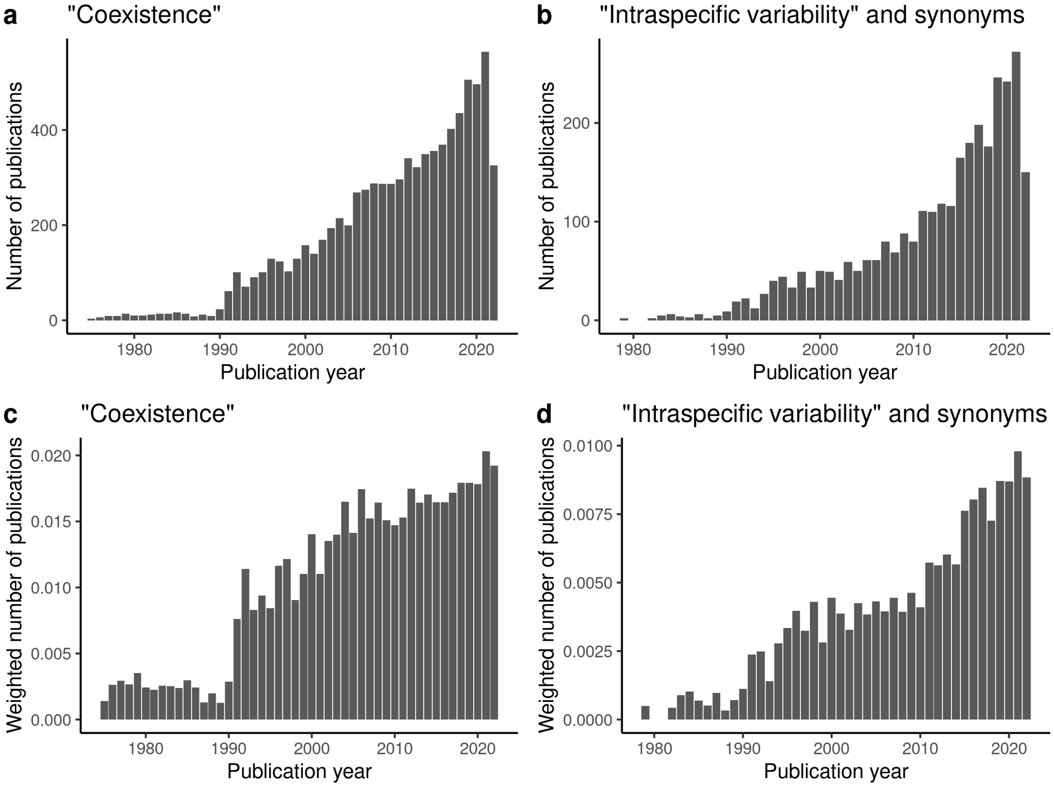

Figure 4: Importance of coexistence and intraspecific variability in ecological research. **a.** Number of publications per year in ecology with the word "coexistence" in title, abstract or key words. **b.** Number of publications per year in ecology with the word "intraspecific variability" and synonyms in title, abstract or key words. **c.** Relative number of publications per year in ecology with the word "coexistence" in title, abstract or key words, *i.e.* numbers of a. divided by the number of publications in ecology in the same years. **d.** Relative number of publications per year in ecology with the word "intraspecific variability" and synonyms in title, abstract or key words, *i.e.* numbers of a. divided by the number of publications in ecology in the same years. The numbers were obtained using Web Of Science, with the following requests. "coexistence": (TS=(coexistence)) AND WC=(Ecology)), gathering 8,337 results on 30/09/2022; "intraspecific variability" and synonyms: ((TS=("intraspecific variability") OR TS=("intra-specific variability") OR TS=("inter-individual variability") OR TS=("intraspecific variation") OR TS=("intra-specific variation") OR TS=("inter-individual variation") OR TS=("intraspecific variance") OR TS=("intra-specific variance") OR TS=("inter-individual variance") OR TS=("individual variance")) AND WC=(Ecology)), gathering 3,095 results on 30/09/2022; Ecology: WC=(Ecology), gathering 608,151 results on 30/09/2022.

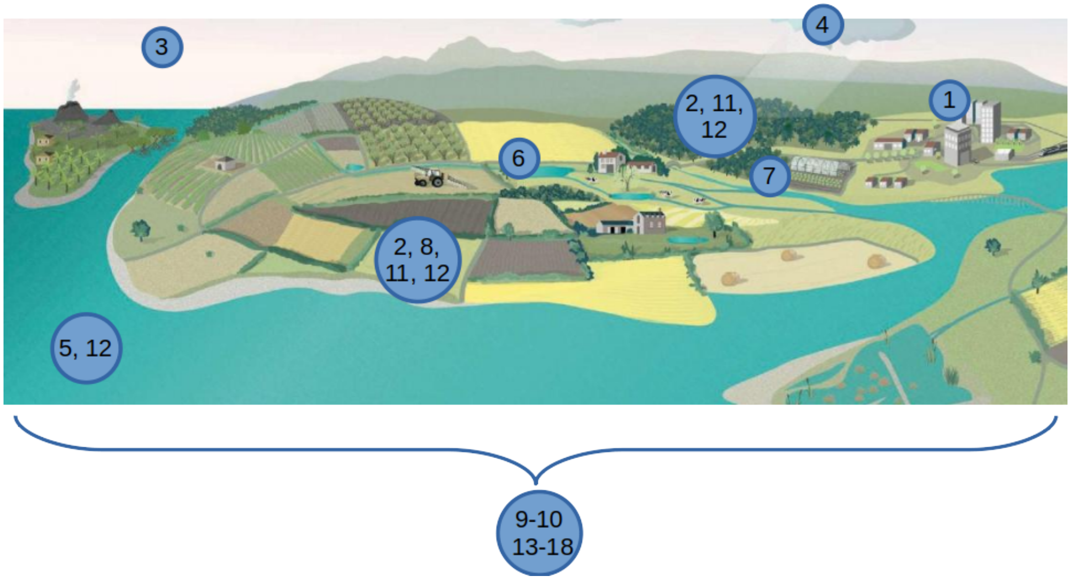

Figure 5: Nature's Contributions to People (NCP) as listed by the IPBES (2019). 1) **Habitat creation and maintenance**: formation and continued production, by ecosystems, of ecological conditions necessary or favourable for living beings important to humans. 2) **Pollination and dispersal of seeds**: Facilitation by animals of movement of pollen among flowers, and dispersal of seeds, larvae, or spores of organisms beneficial or harmful to humans. 3) **Regulation of air quality**: Regulation (by impediment or facilitation) by ecosystems of atmospheric gases; filtration, fixation, degradation, or storage of pollutants. 4) **Regulation of climate**: climate regulation by ecosystems (including regulation of global warming) through effects on emissions of greenhouse gases, biophysical feedbacks, biogenic volatile organic compounds, and aerosols. 5) **Regulation of ocean acidification**: regulation, by photosynthetic organisms, of atmospheric CO_2 concentrations and so seawater pH. 6) **Regulation of freshwater quantity, location and timing**: regulation, by ecosystems, of the quantity, location and timing of the flow of surface and groundwater. 7) **Regulation of freshwater and coastal water quality**: regulation, through filtration of particles, pathogens, excess nutrients, and other chemicals, by ecosystems of water quality. 8) **Formation, protection and decontamination of soils**: formation and long-term maintenance of soils including sediment retention and erosion prevention, maintenance of soil fertility, and degradation or storage of pollutants. 9) **Regulation of hazards and extreme events**: amelioration, by ecosystems, of the impacts of hazards; reduction of hazards; change in hazard frequency 10) **Regulation of organisms detrimental to humans**: regulation, by ecosystems or organisms, of pests, pathogens, predators, competitors, parasites, and potentially harmful organisms. 11) **Energy**: production of biomass-based fuels, such as biofuel crops, animal waste, fuelwood, and agricultural residue. 12) **Food and feed**: production of food from wild, managed, or domesticated organisms on land and in the ocean; production of feed. 13) **Materials and assistance**: production of materials derived from organisms in cultivated or wild ecosystems and direct use of living organisms for decoration, company, transport, and labour. 14) **Medicinal, biochemical and genetic resources**: Production of materials derived from organisms for medicinal purposes; production of genes and genetic information. 15) **Learning and inspiration**: Opportunities for developing capabilities to prosper through education, knowledge acquisition, and inspiration for art and technological design (*e.g.*, biomimicry). 16) **Physical and psychological experiences**: Opportunities for physically and psychologically beneficial activities, healing, relaxation, recreation, leisure, and aesthetic enjoyment based on close contact with nature. 17) **Supporting identities**: basis for religious, spiritual, and social-cohesion experiences; sense of place, purpose, belonging, rootedness or connectedness, associated with different entities of the living world; narratives and myths, rituals and celebrations; satisfaction derived from knowing that a particular landscape, seascape, habitat or species exist. 18) **Maintenance of options**: capacity of ecosystems, habitats, species or genotypes to keep human options open in order to support a later good quality of life. Background image by Lucile Wargniez.

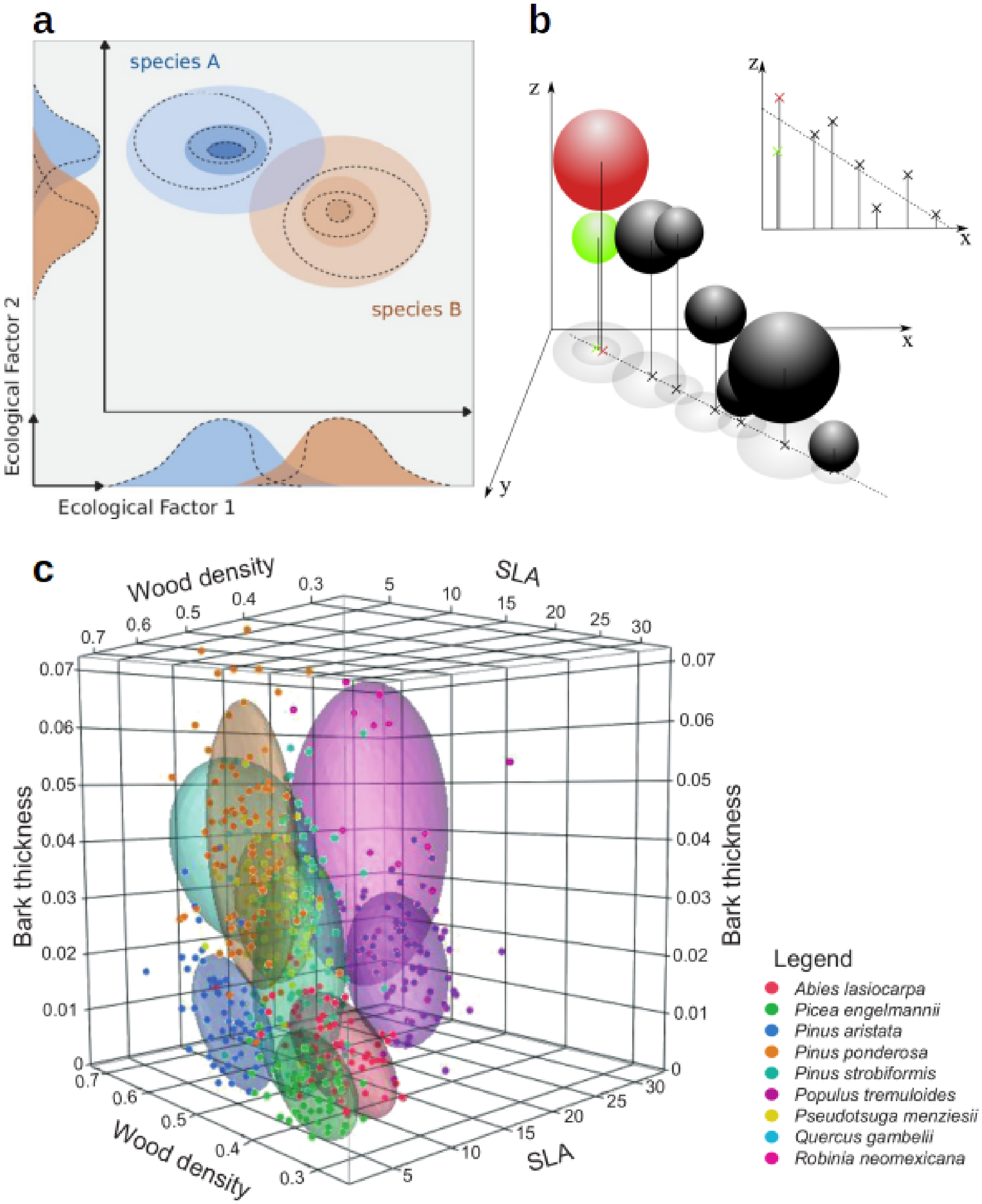

Figure 6: Representations of the ecological niche a. A two-dimensional representation of the ecological niche of two species. Each colour represents the fundamental niche of a species - their performance along the ecological gradients - while the dotted lines show their realized niches, after the effect of biotic interactions (here, competition between the two species for the two ecological factors) are applied. The ecological factors could for instance be light and water availability for plants. Copyright Gaüzère (2016).**b.** A three-dimensional representation of the ecological niche. The third ecological factor Z could be temperature. Adding a niche dimension can reveal the distinction of apparently overlapping niches. Here the niches show a perfect trade-off between axes x and y, and an imperfect trade-off between axes x and z. Copyright Le Bec (2014).**c.** An example in real data of non-overlapping species niches in several dimensions. Copyright Laughlin et al. (2012).

as the importance of the concept of competition in Darwinian theory, led to the development of the concept of ecological niche in the beginning of the 20th century. The ecological niche can generally be defined as what describes a species' ecology, which may be for instance its habitat ("address") or its role in the ecosystem ("profession" or function) (Pocheville 2015). The niche was historically associated either to environmental conditions like temperature that explain speciation with an evolutionary vision, or to the characteristics of species driving community structure and population dynamics like their position in a food web or their specific habitat. The niche concept is tightly linked with the principle of competitive exclusion (Gause 1934; Pocheville 2015; Polechova and Storch. 2008). This principle states that two species, in order to survive concomitantly, should occupy different ecological niche. Otherwise, they compete until the most performing species wins, excluding the loser from the community. The concept of niche has thus played a central role in coexistence theory.

Niche as a hypervolume Hutchinson (1957) describes the ecological niche as an attribute of the species, defined in the space of environmental variables (biotic and abiotic), thus defining a volume in many dimensions - a hypervolume. He broke down this niche concept into two sub-concepts: the "fundamental niche", which is the volume delineated by the limits of species viability, and does not depend on competitors, and the "realised niche", which is the niche actually occupied by the species *i.e.* the volume included in the fundamental niche where the species actually survives (although the realised niche could be larger than the fundamental niche with source-sink dynamics, Pulliam 1988). Therefore, in this framework, ecological niches are dynamic, since the realised niche of a species depends on other species. As an illustration, the realised niche of invasive species can shift as they arrive in a new community (Tingley et al. 2014; Datta et al. 2019; Zhang et al. 2022). By extension, the niche concept also encompasses the ecological requirements of a species and its functional role in the community (Pocheville 2015; Polechova and Storch. 2008). However, those concepts remain highly theoretical. Indeed, Hutchinson's hypervolume is practically impossible to measure in the field since there is potentially an infinite number of dimensions for which measurements can be difficult to determine. Moreover, the distinction between theoretical and realised niche is unclear, since the presence of competitors can be considered as a biotic dimension characterising the fundamental niche (Polechova and Storch. 2008). The definition and measures of ecological niche axes have therefore been further discussed (*e.g.* MacArthur and Levins 1967; Chase and Leibold 2003). Chase and Leibold (2003) notably further defined the niche as the union of the responses (corresponding to Hutchinson's concept of the niche) and impacts of the organism to the ecological factors (sometimes referred to as the 'requirement' and the 'impact' niche, Violle et al. 2007).

Ecological trade-offs Species niches are constrained by bio-physical limits but also by costs, often preventing them to be good at everything. The question of cost is crucial to understand how species' characteristics appear: everything that provides a competitive (and evolutionary) advantage has a cost (*e.g.* in energy, in carbon), and therefore has also a negative impact on fitness (Stearns 1989; Garland 2014, Figure 6b). For instance, producing many seeds increases the fitness of a tree, but the energy that is stored in those seeds will not be available to build defenses against herbivores or pathogens, which has a negative impact on life expectancy (and therefore the fitness) of the tree (there is a trade-off between stress tolerance and fecundity, Muller-Landau 2010). Another important trade-off in forests is growth in high light *vs.* survival in low light (Gilbert et al. 2006), mediated by respiration rates (Loach 1967) or whole-plant biomass allocation strategies (Ntawuhiganayo et al. 2020). Therefore, species can have strategies that follow trade-offs, that are defined by evolutionary constraints. Those trade-offs can foster species coexistence since a single species cannot have all the advantages along all the niche axes or in the presence of any other species and therefore cannot outcompete the other species (Tilman 1982; Kinzig et al. 1999; Livingston et al. 2012).

Based on the concept of ecological niche *i.e.* acknowledging that species have specific ways of life, many mechanisms have been proposed to explain coexistence patterns, some of which are detailed in Box 1 where the focus is on plant species communities.

Box 1: Examples of niche mechanisms

The competition–colonisation trade-off The competition-colonisation trade-off proposed by Levins and Culver (1971) is a canonical example of ecological trade-offs that enable species coexistence through spatial niche partitioning (Livingston et al. 2012, Figure 7b) between coloniser and competitor species. Coloniser or fugitive species efficiently colonise empty habitat patches *e.g.* thanks to high fecundity or dispersal, while competitor species efficiently outcompete other species within sites (*e.g.* through higher survival rates and better resource uptake). The key assumption is that colonisers are bad competitors and vice-versa (Calcagno et al. 2006). In plant communities, this trade-off can be mediated by seed size (Turnbull et al. 2004).

The Janzen-Connell hypothesis Janzen (1970) and Connell (1971) independently hypothesised that host-specific natural enemies (seed predators, herbivores and pathogens) reduce the survival rate of offsprings (seeds, seedlings and juveniles) close to conspecific adults or where conspecific adults density is high. Therefore, a plant would impact more negatively its conspecifics than its heterospecifics, which would limit the density of species in a negative feedback loop, thus favouring rare species and promoting species coexistence (Comita et al. 2014, Figure 7a). Here, the focal niche dimension is thus the biotic interaction with natural enemies.

The intermediate disturbance hypothesis In the late- 1970's, several publications by Grime, Horn and Connell presented a "humped-backed graph" (Figure 7c) highlighting the effect of the frequency of disturbance in maintaining species diversity (Wilkinson 1999). Indeed, an intermediate level of disturbance in an ecosystem enables to go past the pioneer phase of the succession (which is be the only phase if disturbance is frequent) whilst avoiding the competitive exclusion of species that are not adapted to the late phases of the succession (which is the case if disturbance is rare). In tropical forests, gap-dynamics are an example of this mechanism: pioneer, shade-intolerant species can thrive in gaps while shade-tolerant species can thrive elsewhere (Molino and Sabatier 2001), relating this mechanism to the growth in high light *vs.* survival in low light trade-off (see above).

The regeneration niche hypothesis Grubb (1977) highlighted the importance of an overlooked aspect of the ecological niche, the specific conditions required to go through a species' life cycle, to explain species coexistence. Indeed, the conditions influencing the production of seeds, their germination and dispersal, the establishment of the juvenile and its onward growth vary greatly in space and time (*e.g.* as a function of soil water content, gap size, litter depth) and can combine in a high number of ways. These species-specific conditions, called regeneration niche, determine the chance of success in the replacement of one mature individual by a new one of the next generation, and is therefore a key coexistence mechanism.

The storage effect hypothesis Chesson and Warner (1981)) showed in a lottery model, that varying environmental conditions enabled the coexistence of species with different birth rates, death rates and ability to find and secure space. This relies on the fact that each species has a unique response to varying environmental conditions and that each population stores the gains in good years or habitats, enabling to survive losses in bad years or habitats. Therefore, species perform better in different spatio-temporal windows, which reduces competition between species and thus competitive exclusion.

The resource ratio hypothesis Tilman (1982) formalised the hypothesis that if several species are competing for a single limiting resource, then the species that can survive at the lowest equilibrium resource level (*i.e.* has the lowest resource ratio denoted R*) outcompetes all other species. Therefore, under this hypothesis, multispecies coexistence requires that each species has the lowest R* on one of the resources and that there is sufficient variation in resource ratios across the landscape.

Other niche-based mechanisms (not detailed here) encompass for instance microbial mediation (Hodge and Fitter 2013), facilitation (Vellend 2008) or allelopathic defenses (Mougi 2013).

I.2.b. The neutral theory

Hubbell (2001) presented an alternative to the niche theoretical framework: he proposed that species (niches) differences, although observable (Hubbell 2005), do not drive community dynamics, which are rather determined by events considered (or a least represented) as stochastic like mortality, recruitment, migration, and speciation. Under this assumption, species in the same trophic level are therefore functionally equivalent, *i.e.* have the same per capita vital (mortality, fecundity, dispersal) and speciation rates (Hubbell 2005, Figure 7d). Therefore, niche multidimensionality is not assumed. Rather, the functional equivalence is a minimal assumption to which complexity is gradually added in order to understand which dimensionality is necessary to reproduce observed ecological patterns (Hubbell 2005). The role of competition is not as central as in the classical niche theory (Hubbell 2005), and species follow a slow random walk to extinction (called ecological drift), which is compensated by speciation and immigration from a regional species pool (Gravel et al. 2006). Tested against data, this theory was able to reproduce some observed community patterns, like species rank abundance with few dominant species and many rare species in tropical forests. However, it was and to some extent still is highly controversial among ecologists. Indeed, it tips over the foundation of the still young scientific field that ecology is, and questions the significance of decades of naturalistic observations and theoretical developments (Chave 2004). However, it was able to stimulate scientific debate, and to propose a null-hypothesis for species functional differences (although controversial too, Clark et al. 2007). While there were attempts at reconciling niche and neutral theories in a niche-neutrality continuum (Chave 2004; Gravel et al. 2006), this continuum has been criticised because it is a knowledge- rather than an ecological-continuum (Clark et al. 2007).

I.2.c. The modern coexistence theory framework

Chesson (2000b) provided a framework to analyse the coexistence mechanisms, in parallel with the niche *vs.* neutral framework, which can be more philosophical than operational (Chave 2004, see also the importance of schools of thoughts in ecology in Lewin 1983; this paper playfully entitled "Santa Rosalia was a goat" prefigures the neutral *vs.* niche debate). Namely, he proposed two types of mechanisms. On the one hand, stabilizing mechanisms increase the relative importance of intraspecific competition compared to interspecific competition, and therefore tend to give an advantage to rare species through density-dependent processes. These mechanisms are thus necessary (but not sufficient) for recovery from low density (Chesson 2000b). Examples of these mechanisms are storage effects, resource-use related trade-offs or the Janzen-Connell hypothesis. On the other hand, equalizing mechanisms reduce the fitness differences between species, making competition less asymmetrical. Examples are competition-defense tradeoffs (Chesson 2018) and mortality-related trade-offs (Chesson 2000b). Some mechanisms can also have both stabilising and equalising properties. For instance competition-colonisation trade-offs can have stabilising or equalising effects depending on the scale of observation (Cadotte 2007). Indeed, mathematical models of destabilising fitness differences and stabilising niche differences share terms, and changes in an attribute can be correlated with changes in another attribute (Turcotte and Levine 2016. While stabilising mechanisms promote stable coexistence and equalising mechanisms transient coexistence, equalising mechanisms can enable stable coexistence when stabilising mechanisms are weak, because the fitness differences that stabilising mechanisms have to offset are smaller; similarly the presence of stabilising mechanisms is not a sufficient condition for stable coexistence (Chesson 2000b).

Many of the ecological hypotheses and theoretical frameworks presented above were elaborated thanks to mathematical models, which we are now going to explore.

I.3. Role of models in the study of species coexistence

I.3.a. What is a model and why is it useful?

Models are formal or material constructions aiming at representing something real or fictive (Varenne 2014). In this definition, words are, in a way, models, since they enable us to represent an observed reality. In science, models are mostly formal, *i.e.* symbolic, logic or more often, mathematical constructions: an equation, an algorithm, *etc.* (Varenne 2014). Minsky (1965) defined models this way: "To an observer B, an object A* is a model of an object A to the extent that B can use A* to answer questions that interest him about A.". Therefore, models can be facilitation tools to study questions about real systems (Varenne 2014).

In ecology, models have been used increasingly since the 1970s as instruments to understand the properties and characteristics of ecosystems. More precisely, ecological models can be used to survey ecosystems (*e.g.* survey the number of individuals in a population), to reveal properties of ecosystems, to establish research priorities, and to test scientific hypotheses (Jorgensen 2016), or to make predictions under different scenarios (*e.g.* the effect of different global change scenarios on

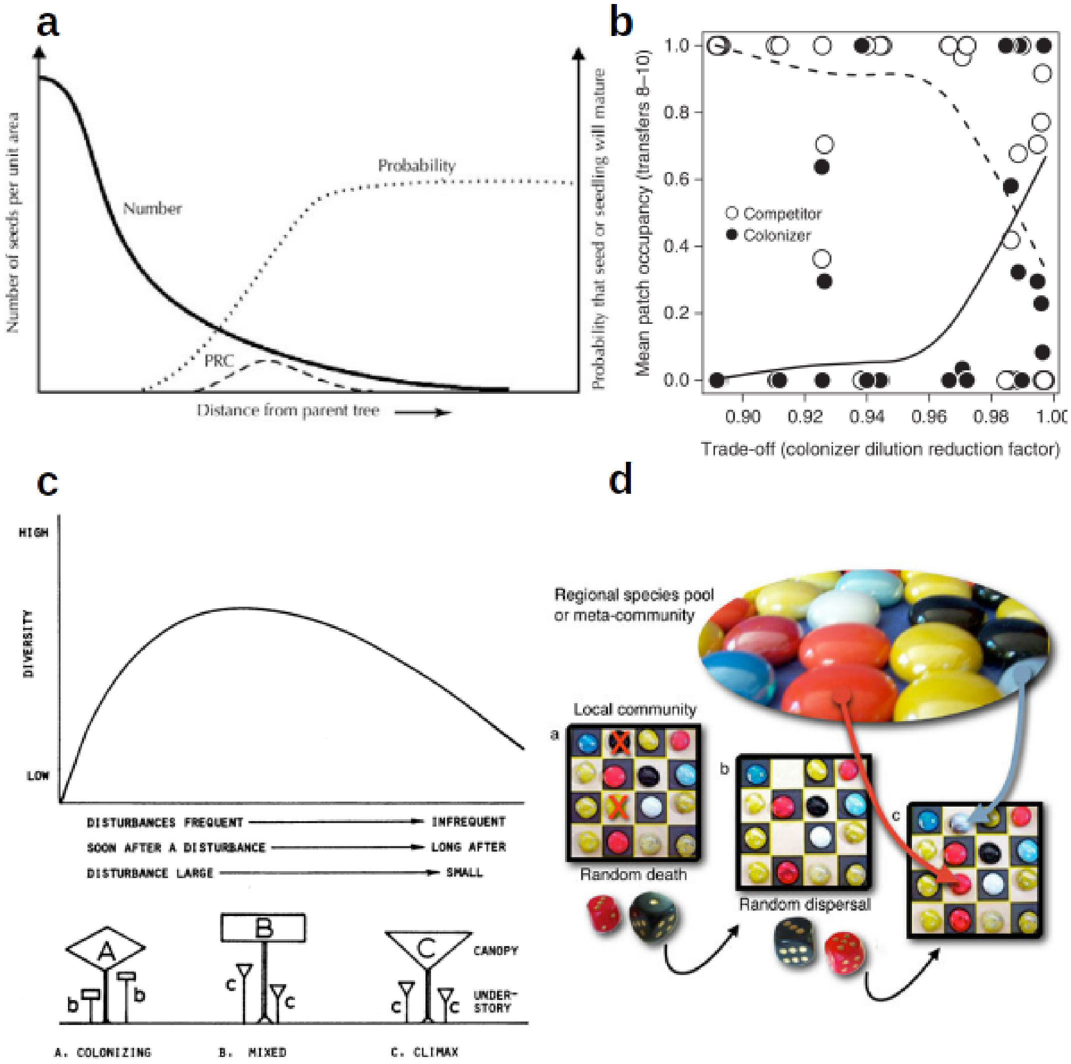

Figure 7: Four coexistence mechanisms a. The Janzen-Connell hypothesis. Near a parent tree, seedling are rarely recruited because the high density of seeds and seedlings attracts species-specific natural enemies. As the number of seeds often decreases with distance to the parent, seedlings are only recruited in a reduced zone at an intermediate distance from the parent tree (the PRC = Population Recruitement Zone). Copyright Janzen (1970); **b.** An example of colonisation-competition trade-off. Observed trade-off in a controlled experimental metacommunity of two *Pseudomonas* bacterial strains. Copyright Livingston et al. (2012). *Remark*: this figure does not concern plants but was chosen for its clarity to illustrate the mechanism. See *e.g.* Turnbull et al. (2004); Muller-Landau (2010) for plant-related figures. **c.** Illustration of the intermediate disturbance hypothesis in tropical forests. Copyright Connell (1978). **d.** A didactic illustration of neutral theory. Random death an random dispersion drive species abundances in the absence of differences between species. Copyright Harpole (2010).

biodiversity, IPBES 2016). Models are therefore useful experimental tools (Jorgensen 2016) but are not reality: there is no “correct” model (Box 1976). By essence a model is always “wrong” or unrealistic, in that the modeller has to make choices.

There are two major types of ecological models, analytical models and simulation models (Grant and Swannack 2008). While analytical models describe the studied system by mathematical equations which behaviour are well-known, simulation models use numerical computation when analytical solutions are difficult or impossible.

In both cases, models enable to explore ideas that are difficult to field-test, for instance for logistical reasons (Jackson et al. 2000). In the case of plant ecology, models are widely used to predict community dynamics under conditions that were not experienced in the field, or that were not extensively recorded (*e.g.* predictions of the future trajectory of an ecosystem under various climate change scenarii or of the consequences of a disturbance on the dynamics of a population). For instance, to obtain empirical data on the reaction of long-lived organisms like trees to changing environmental conditions, experiments and field monitoring should extend over several decades or even beyond the lifespan of the observer. Moreover, the complex interplay between the many determinants of individual ecological responses like tree growth make empirical tests difficult to design and realise to mirror accurately changes occurring in the field (Maréchaux 2016 p.21). In the context of a rapid climate change, and given the complexity of ecosystems, ecological modelling is an essential tool for ecologists. In the case of species coexistence, models enable to build and test hypotheses.

I.3.b. Some insights of models about species coexistence

Coexistence theory has long been tackled using theoretical models (Kingsland 1995), because the data necessary to understand and disentangle the mechanisms of species coexistence are difficult to obtain (*e.g.* species abundances or individual-level demographic rates and functional traits at different life stages with the corresponding environmental variables captured at the relevant scale and over a relevant period), and because models enable a clear formalisation of hypotheses prior to designing experimental designs to test it. Indeed, many of the coexistence hypotheses presented above rely on theoretical models that were then tested using empirical data - although most mechanisms were proposed following naturalistic observation (intervention of Daniel Janzen at the 2021 ATBC conference, interview of Peter Grubb, 2015). More precisely, models of coexistence aim at gathering the minimal ingredients needed to generate coexistence rather than at being realistic, in order to understand what the sufficient conditions for coexistence are (mostly *in silico*). The next step is to test if those conditions are present in data from the field or to from experiments.

For instance, much of the niche theory was developed following the historical Lotka-Volterra competition model (Pocheville 2015), which is an analytical model using differential equations to represent the dynamics of several populations competing for the same resource. Another example is Tilman’s consumer-resource competition model that relies on a very theoretical species parameter R^*, the minimum resource level required to maintain the population, which was inspired by Michaelis-Menten curves. More recently, Hubbell’s neutral theory was proposed as a null-model in ecology, *i.e.* an over-simplified general model to which empirical data can be confronted.

These major ecological models have however been using mean species attribute values. However intraspecific variability - the variability in attributes between individuals of the same species - is acknowledged to be high and ecologically important (Violle et al. 2012).

II. Intraspecific variability and species coexistence

In community ecology, the role of intraspecific variability in species coexistence was introduced *via* the concept of limiting similarity, which posits that coexistence depends on the level of niche overlap, quantified as the ratio of differences in species niche means to intraspecific niche widths (MacArthur and Levins 1967). However, much of community ecology theory and data analysis adopted a "mean field approach" that relies on the assumption that intraspecific variability is ecologically negligible compared to interspecific differences (Bolnick et al. 2003; Violle et al. 2012; Westerband et al. 2021), and discussion on intraspecific variability receded between the 1980s and the 2000s (Bolnick et al. 2003; Violle et al. 2012).

While intraspecific variability has largely been ignored in classical community ecology studies and theories, it has long been recognised as an important feature of the living world; notably, humans have been selecting the most interesting phenotypes to domesticate crops for centuries (Westerband et al. 2021) and intraspecific variability is known to be the raw material of evolution (Bolnick et al. 2003; Violle et al. 2012) and is a central topic in population ecology. Moreover, over the last decades, intraspecific variability has come back to the spotlight in community ecology too, notably thanks to studies showing its quantitative importance and ubiquity in natural communities.

Intraspecific variability has been the subject of hypotheses concerning its role in species coexistence. From now on, we focus on plant communities unless specified otherwise.

II.1. Observed intraspecific variability in communities

Intraspecific variability can be observed at different levels. Notably, it can be assessed between populations of the same species, or within a single population, and even within a single individual (due to temporal changes but also to differentiation, *e.g.* light- and shadow leaves). Since we focus on species coexistence, we will concentrate on the community level, without developing the population level, and we ignore the intra-individual level (although it is partially accounted for when structuring variability in time).

Siefert et al. (2015) reported in a global meta-analysis that on average, intraspecific trait variability accounted for 25% of total trait variation within plant communities (Figure 8e) while Poorter et al. (2018) found that 44% of total trait variability was observed within the species for functional traits related to growth and defense of tree saplings in an Amazonian tropical rainforest. Intraspecific variability has also been found to be high in growth (*e.g.* 63% of tree growth variation in a monsoon forest in South-East Asia, Le Bec et al. 2015; Figure 8b). Intraspecific variability can even be higher than interspecific variability (*e.g.* 48 % of total variance *vs.* 21% for leaf mass area and 35% for leaf dry matter content in trees of lowland tropical forests in Central America, Messier et al. 2010). However, the part of variability accounted by intraspecific variability varies among attributes and species (Albert et al. 2010; Westerband et al. 2021). For instance, native and non-native invaders show different patterns of intraspecific variability, which is very high in leaf mass area but lower in wood density (Westerband et al. 2021).

Moreover, estimates of intraspecific variability are largely biased. Indeed, they are often based on few individuals, and the most frequently used metric to assess the extent of intraspecific variability, namely the coefficient of variation (ratio of the mean and the variance of the sample), can be biased and frequently underestimated (Westerband et al. 2021). Besides, research biases lead to limited evaluation of intraspecific variability, since most studies focus on few plant traits (*e.g.* leaf morphological traits like specific leaf area and leaf mass area, leaf chemical traits like nitrogen and phosphorus concentrations and plant height) while hydraulic, root or reproductive traits are

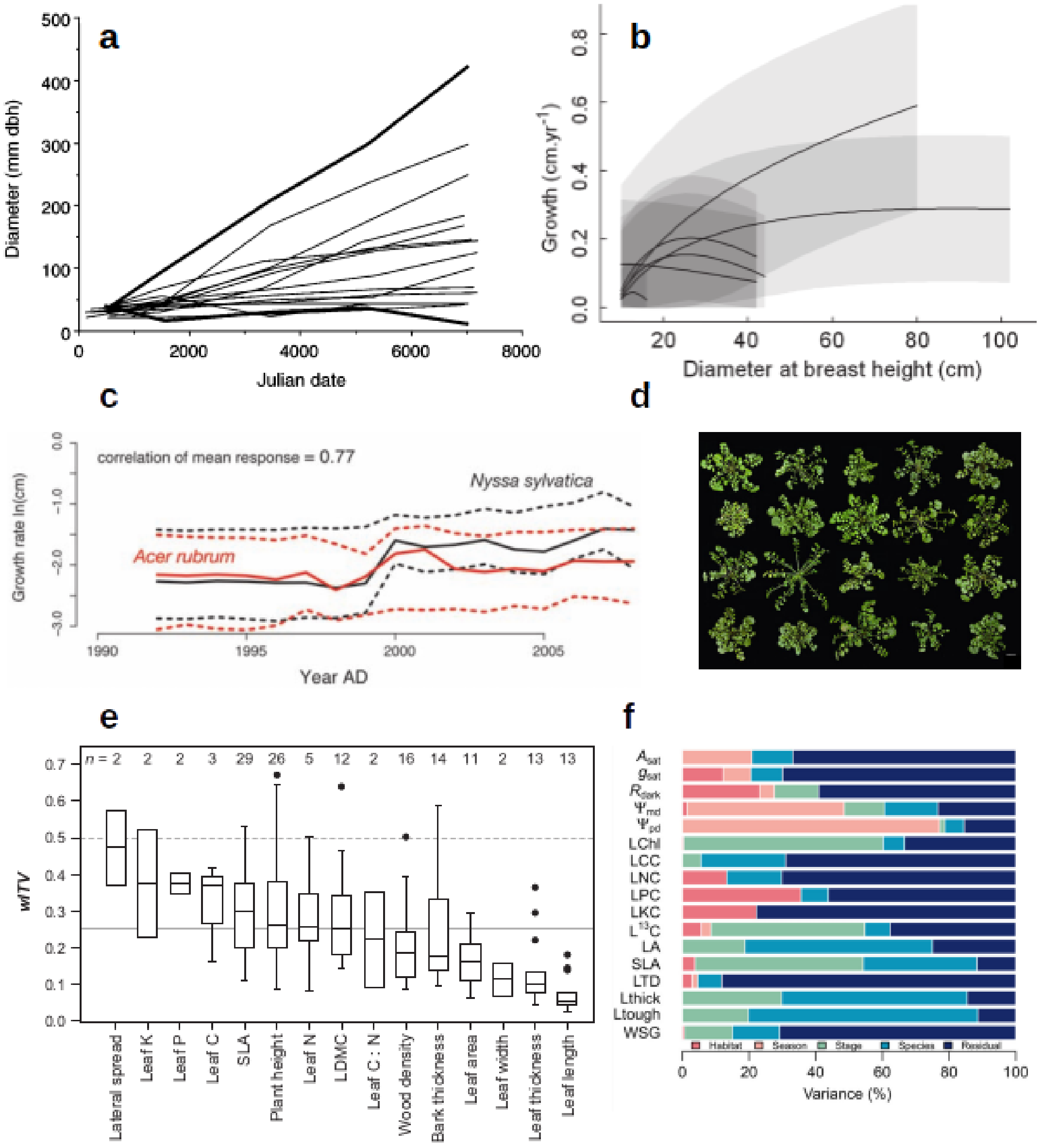

Figure 8: Visualisation of the extent of observed intraspecific variability a-c: in growth; **d**: in visual appearance; **e-f**: in functional traits. **a.** Growth rates of 15 individuals of the pioneer neotropical species *Jacaranda copaia*. Copyright Hubbell (2005). *Remark*: Interestingly, the high variability of growth rates within the species spanning interspecific differences is used as an argument in favor of neutral dynamics. **b.** Growth responses to tree size of six tropical species (*Vateria indica*, *Humboldtia brunonis*, *Myristica dactyloïdes*, *Knema attenuata*, *Palaquium ellipticum* and *Dipterocarpus indicus*). Shown are growth at standardised conditions (solid lines) and the 95th percentile of the estimated distribution for each species (envelops). Copyright Le Bec et al. (2015). **c.** Growth rate of two temperate tree species (*Acer rubrum*, red and *Nyssa sylvatica*, black). Shown are the median (solid lines) and the 95% variation among individuals (dashed lines). Copyright Clark (2010). **d.** Morphological variation in *Cardamine hirsuta*. Copyright Univ. Bochum (`https://www.ruhr-uni-bochum.de/dfg-spp1529/Seiten/PG_Tsiantis_HA6316_1-3.html`). **e.** Intraspecific variability of 15 plant functional traits within communities as reported across 33 studies. Copyright Siefert et al. (2015). **f.** Variance partitioning of trait values across habitat, season, developmental stage, and species identity for 17 traits of four *Micropholis* (Sapotaceae) species sampled in French Guiana across broad environmental gradients. Copyright Fortunel et al. (2020).

rarely studied (Westerband et al. 2021). On the contrary, for animal populations, a “file-drawer effect” that tends to consider insignificant intraspecific variability as unworthy of publication has been suspected (Bolnick et al. 2003), a phenomenon that could also emerge in plant ecology since intraspecific variability is now a “trendy” topic in ecology (Figure 4). These biases not only prevent from good estimation of the extent of intraspecific variability, they also impede the understanding of whole-plant functioning strategies (Westerband et al. 2021).

Observed intraspecific variability is thus ubiquitous and often high in communities. It is therefore important to know what generates this variability to then explore its effect on community dynamics.

II.2. Sources of intraspecific variability

Intraspecific variability results from two sources: genotypic variation and phenotypic plasticity, *i.e.* the non-genetic variation in trait expression within genotypes (Albert et al. 2010; Violle et al. 2012; Westerband et al. 2021. Sources of intraspecific variability can also be categorised as heritable *vs.* non-heritable (Moran et al. 2016).

Genotypic variation is heritable and can arise from local adaptation to a particular habitat, from genetic drift in a population, random mutations or developmental noise, while phenotypic variation is not heritable and is due to environmental heterogeneity (Westerband et al. 2021). These two sources are however not independent from each other. Indeed, the environment (both biotic and abiotic) shapes genotypes on the evolutionary time-scale though adaptation while phenotypic plasticity has a genetic basis (Nicotra et al. 2010; Westerband et al. 2021). Moreover, intraspecific variability can result from epigenetic variation, *i.e.* molecular processes that can alter gene expression without any change in underlying genetic code, and that can be driven by environmental cues (Moran et al. 2016; Westerband et al. 2021). This epigenetic variation can be heritable, but not necessarily, and over an intermediate time-span (1-5 generations, Moran et al. 2016).

Ontogenic trait variation, resulting from shifts in trait expression throughout development and that can be coordinated by environmental cues, can also be considered as an important source of intraspecific variability (Westerband et al. 2021) although traits are mostly measured within a life-stage or age class (Violle et al. 2012). Ontogenic trait variation can be difficult to disentangle from environmental variation (Westerband et al. 2021; Fortunel et al. 2020; Barthélémy and Caraglio 2007).

Overall, the level of observed intraspecific variability is governed by gene flow on the one hand (controlled by mutation, drift, migration and selection, Vellend and Geber 2005), and environmental heterogeneity on the other hand.

II.3. Hypotheses regarding the effect of intraspecific variability on coexistence

Intraspecific variability can have cascading effects on higher ecological scales (population, community, ecosystem, and even the global scale, Westerband et al. 2021, Figure 10a). Indeed, the individual level is the level at which interactions with the local biotic and abiotic environment happen, for instance neighbours competition and facilitation processes (Violle et al. 2012). Therefore, shifts in attributes like functional traits or components of performance, whether they are due to genetic variability or phenotypic plasticity, can have effects that propagate on higher ecological levels. Trait-performance relationships are required to link intraspecific variability to higher-order

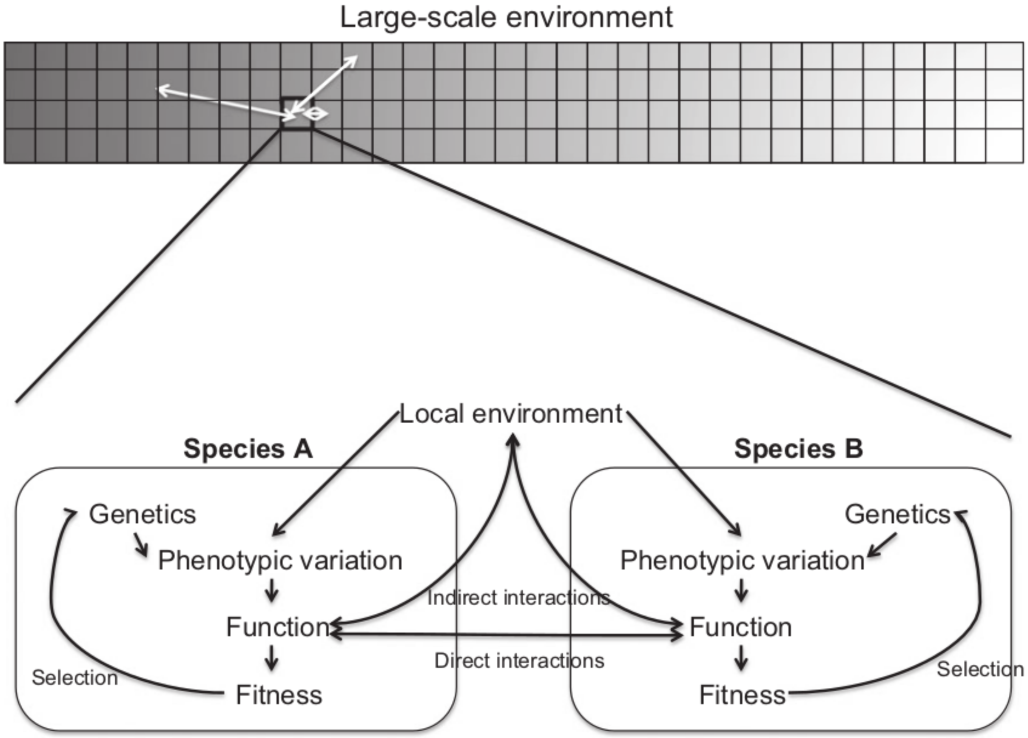

Figure 9: Sources of intraspecific variability "At the landscape scale (top), trait variation is shaped by large-scale environmental gradients. Within local sites (bottom), phenotypic variation in each species is shaped by genetic variation and by plastic responses to the local biotic and abiotic environment. This variation affects species interactions with one another and with the environment, ultimately impacting individual fitness. Differences in fitness feed back to affect genetic variation. Local genetic variation is also affected by dispersal between populations (white arrows at top)." Copyright Moran et al. (2016).

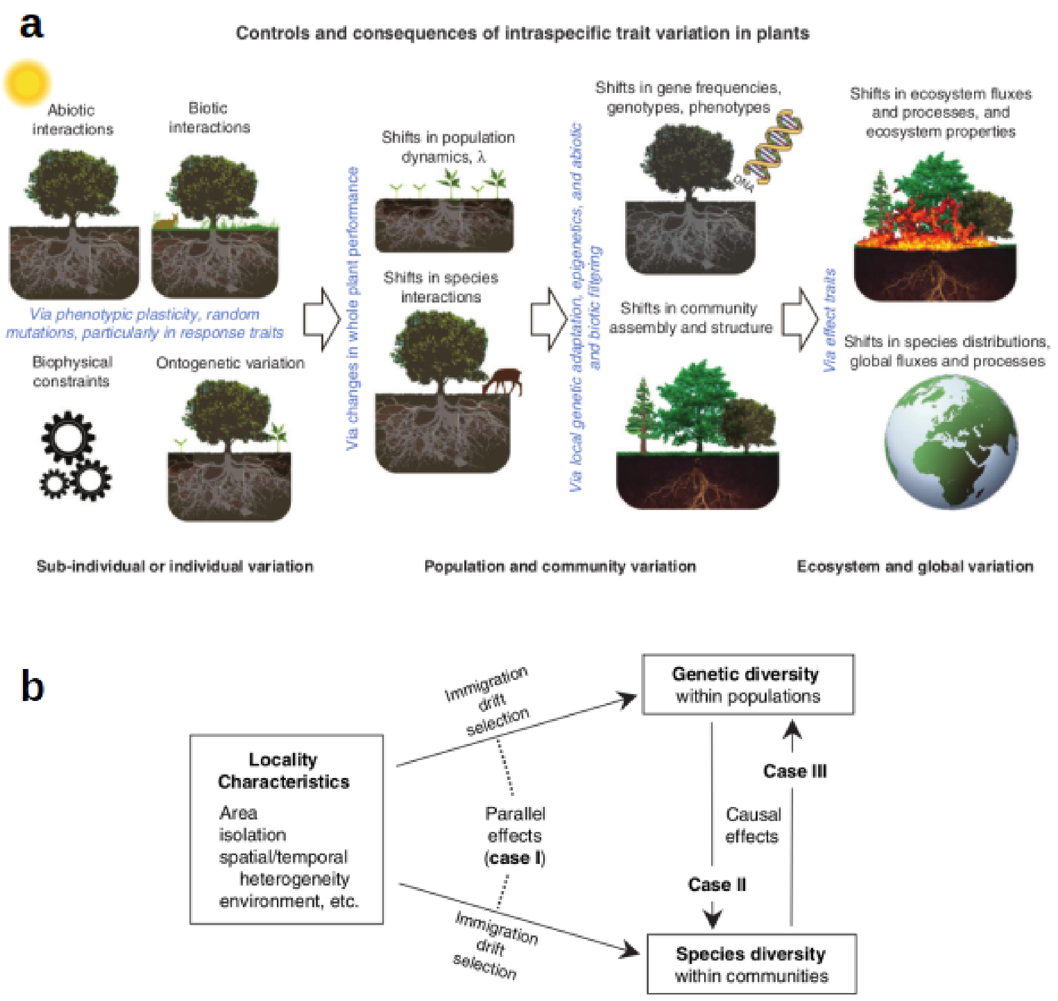

Figure 10: Relationships between the individual level and higher ecological levels. **a.** General framework, showing potential cascading effects and feed-backs from the individual to the global scale. Copyright Westerband et al. (2021). **b.** Framework of the relationships between genetic diversity within populations and species diversity within communities. Copyright Vellend and Geber (2005).

ecological processes (Westerband et al. 2021; Hart et al. 2016; Stump et al. 2022) since individual performances drive population dynamics and species interactions (Westerband et al. 2021), although trade-offs between components of performance across a plant's life time can weaken the apparent link between individual performance and population performance metrics (Westerband et al. 2021). For example, intraspecific variability in functional traits can have significant effects on ecosystem functioning (*e.g.* nutrient and carbon cycles, response to herbivory and water cycling, Albert et al. 2010; Westerband et al. 2021), intraspecific variability in seed dispersal influences population dynamics and community assembly and composition (Westerband et al. 2021). Intraspecific variability can also have consequences for plant-herbivore interactions, plant-microbial interactions and invasions (Westerband et al. 2021). Intraspecific genetic variability can also affect species diversity (Vellend and Geber 2005, Figure 10b) or productivity (Moran et al. 2016). Importantly, a recent meta-analysis has shown that the ecological effect of variation within a species (intraspecific effect) can be comparable or even stronger than the effect of replacement or removal of this species (species effect) (Des Roches et al. 2018).

Several hypotheses have been proposed concerning the role of intraspecific variability in species coexistence. These hypotheses can be contextualised with understandings of intraspecific variability and ecological theory frameworks.

The common understanding of intraspecific variability is that it blurs the differences between species (Lichstein et al. 2007; Hart et al. 2016). However, two diverging hypotheses stem from this approach: (i) following the classical niche approach, intraspecific variability increases niche overlap and therefore interspecific competition (*i.e.* weaken stabilising coexistence mechanisms *sensu* Chesson), thus favouring competitive exclusion (Gause 1934; MacArthur and Levins 1967); (ii) following the neutral theory approach, intraspecific variability blurs species differences, making the dynamics more neutral (*i.e.* support equalising coexistence mechanisms *sensu* Chesson), thus promoting transient coexistence. Under this second hypothesis, intraspecific variability provides opportunities for species to do better or worse than their average performance, leading to local competition inversions (*i.e.* at a point in space and time, the species that is best performing on average does not necessarily outperform other species), which prevents or slows down competitive exclusion and enables species with lower average performance to be maintained in the community (Vieilledent et al. 2010; Courbaud et al. 2012). Moreover variability in a given attribute could influence the strength of stabilising and equalising mechanisms at the same time (Turcotte and Levine 2016).

These hypotheses have been tested using data analysis as well as theoretical models.

II.4. Tests of those hypotheses

Here we present some of the empirical and theoretical tests concerning the effect of intraspecific variability on species coexistence. We only present studies concerning plant communities and coexistence of competitors (species that belong to the same trophic level).

II.4.a. In data

Experimental studies on the effect of intraspecific variability on community dynamics remain rare and mostly focus on genetic rather than trait variability (Hart et al. 2016).

Concerning genetic intraspecific variability, most empirical studies found a positive relationship with species coexistence. In a review of theoretical and empirical studies, Vellend and Geber (2005) note that empirical data predominantly show positive relationships between species diversity and genetic diversity within populations. Later studies confirmed this tendency; for instance Lankau and Strauss (2007) found using combined observations of natural populations, quantitative genetics and field experiments that genetic intraspecific variability in concentration of an allelopathic secondary compound in *Brassica nigra* was necessary for the coexistence with its competitor species. Fridley and Grime (2010) applied a gradient of intraspecific genetic diversity in several communities and found a connection between intraspecific genetic diversity and final species richness. In a more recent review, Ehlers et al. (2016) highlighted that empirical studies show that genetic intraspecific variability can affect species coexistence via several mechanisms. They organised effects of genetic intraspecific variability on species coexistence in four categories. First, it can be a source of micro-environmental variation, *e.g.* through chemical compounds or plant architecture. Second, it can promote both equalising (by decreasing the overall intensity of interspecific competition) and stabilising (*e.g.* by mediating allochemical concentrations) coexistence mechanisms. Third, recognition of related individuals, probably through intraspecific variation in root exudates, can impede or foster coexistence depending on kin-facilitation or competition. Finally, local adaptation can make environments less stressful which impacts species interactions.

Concerning intraspecific variability in functional traits, the empirical results are less abundant and less consistent. For instance, Jung et al. (2010) found a positive effect of intraspecific variability at the population level in SLA, LDMC and plant height on species coexistence along a flooding gradient, due to both habitat filtering and niche differentiation. In contrast, using a gradient of species diversity in forest communities (from boreal to tropical), Bastias et al. (2017) found that intraspecific variability in leaf size and SLA was relatively invariant in regard to species richness, leading to higher functional similarity with higher species richness. Interestingly, Turcotte and Levine (2016) highlighted in a review that results on the effect of phenotypic plasticity on species coexistence were unclear and contradictory, that studies were often lacking theory, and that there could be a confirmation bias concerning the positive effect of phenotypic plasticity on species coexistence since it is the common hypothesis.

Overall, these results do not enable to conclude on a clear role of intraspecific variability in species coexistence. Although empirical data are fundamental to ecological understanding of natural communities, gathering experimental data or designing experiments to assess the effect of intraspecific variability on species coexistence is difficult. An alternative way to gather new insights on this topic is to use models, which can be data-based or fully theoretical.

II.4.b. In models

In a review of theoretical models, Bolnick et al. (2011a) presented six mechanisms by which intraspecific variability could impact community structure or dynamics. While four of those mechanisms do not necessarily rely on genetics, many examples they present concern genetic intraspecific variability. The first mechanism presented is *non-linear averaging*, also called Jensen's inequality, which is the property of non-linear functions to produce averages ($\overline{f(x)}$ with a trait x) that are not equal to the function evaluated at the mean trait value ($f(\overline{x})$). Therefore, when this nonlinear function is an ecological interaction that varies with a trait, variation around the trait mean can alter the average interaction strength. Interestingly, if the function links a competitive capacity with a component of fitness and is concave-up, it gives the best competitor a disproportionate advantage, making competitive exclusion more likely, while a concave-down relationship could have the opposite effect. The second mechanism is *increased degree*, which is the potentially higher number and lower strength of interspecific interactions: more variable species are expected to interact with more species, thus increasing the connectivity within the network of the community, but their interactions are expected to be weaker. Changes in the number and strength of network connections can impact ecological dynamics. More specifically, more numerous but weaker interactions could have a stabilising effect on ecological dynamics. The third mechanism is the *portfolio effect*, which is the buffering of temporal or spatial variations of a population density through negative covariances among phenotypes within species, thus stabilising the total population size (which can prevent from extinction). The fourth mechanism is *phenotypic subsidy*, which is the coupling of dynamics of different phenotypes. This mechanism changes the equilibria each phenotype would experience alone, and it can be, but is not always, stabilising. The fifth mechanism is *adaptive eco-evolutionary dynamics*. Indeed, evolution can occur on the same timescales than population dynamics and trigger feedbacks between ecological processes and trait evolution. Heritable trait variation can therefore allow evolution of traits and adaptation to the environment, which alters ecological interactions. The last mechanism is *trait sampling* due to demographic stochasticity and genetic drift, which is more pronounced in small populations and impacts trait values and distribution, therefore altering population dynamics.

In Table 1, we present a non-exhaustive list of theoretical models that tested the effect of intraspecific variability on species coexistence. Like in data, the inconsistent results of these tests models do not enable to conclude on the role of intraspecific variability in species coexistence. In most of those models, intraspecific variability has been introduced as a random noise around species parameters, which necessarily increases the similarity among heterospecific individuals (but see Uriarte and Menge 2018 and especially Banitz 2019); however, this way to implement intraspecific variability and which ecological meaning of intraspecific variability it conveys are rarely discussed.

Table 1: Examples of theoretical studies that incorporated intraspecific variability in theoretical models to assess its role on species coexistence or community dynamics. IV = intraspecific variability; ITV = intraspecific trait variation; DBH = diameter at breast height; PFT = plant functional type.

Begon and Wall (1987)	Not specified	Two species competition Lotka-Volterra model	Competitive ability (intra- and/or inter-specific)	Seven classes are defined in the species using a symmetric, pseudo normal distribution. For inter- and intraspecific competition respectively, increments between successive classes are a percentage of the mean value or a number added to the mean value.	Positive or neutral	Variation in intraspecific competitive ability alone does not have consequences on coexistence. Variation in interspecific competitive ability enhances species coexistence. The effect is stronger with variation in intraspecific competitive ability. Enhanced coexistence is mostly mediated by the variation of the effect of the superior competitor on the inferior competitor.
Vellend (2006)	Plant communities	50-species Lotka-Volterra-based competition model with competition for space and clonal reproduction	Optimum in a 1-dimensional niche space	Two components of IV: 1) potential phenotypic range *i.e.* species niche width; 2) the number of genotypes in this range. Potential genotypes are equally spaced and the actual number of genotypes is randomly drawn if it is lower than the number of potential genotypes.	Positive	Both components of IV increase species diversity.
Lichstein et al. (2007)	Plant communities	Two-species model of plant competition	Competitive ability in juveniles	Performance values are drawn independently from a species-specific probability distribution (uniform or Gaussian).	Variable	ITV can have a positive impact if there is a mean-variance (of performance) trade-off, but it depends on competitor density.
Yamauchi and Miki (2009)	Plant species (annual)	Model from Vellend (2006) where reproduction can be sexual and not just clonal. Environmental fluctuations in growth rate can be temporal and affect all niche positions simultaneously or niche dependent (conditions between niche positions vary over the year and are correlated between neighbouring niches).	Optimum in a 1-dimensional niche space	Niche width around mean 1-dimensional niche position. There are three niche width levels.	Variable	Niche width generally has a positive effect on species coexistence. Environmental variation is often necessary to have this effect.
Vieilledent et al. (2010)	Trees (Abies alba and Picea abies in nine forest stands of the western Alps)	Hierarchical bayesian, spatially explicit, data-based radiation transmission model on real stands	Allometric relations (heigh-DBH, crown height - tree height, crown radius-DBH)	Individual random effects were drawn in a normal distribution of mean zero with a variance of either zero or an inferred value.	Positive	IV in tree allometry modulates species' light-intercepting ability, generating heterogeneous light conditions under the canopy, with high light micro-habitats that may promote the regeneration of light-demanding species and slow down successional dynamics.

Study	Studied system	Model description	Trait on which IV is applied	Implementation of IV	Overall consequences of IV on coexistence	Detailed consequences of IV on coexistence
Courbaud et al. (2012)	Plant communities (trees)	Two-species competition–colonisation patch data-based model of vegetation with intraspecific variability in juvenile growth	Juvenile growth	Juvenile growth is drawn in a lognormal distribution with mean and standard deviation depending on the species. There is either no standard deviation or an inferred standard deviation.	Variable	IV shifts the trade-off between fecundity and competitive ability necessary for coexistence because it reduces interspecific competition asymmetry. IV disproportionately favours the most fecund species. It promotes coexistence when it prevents the exclusion of a fecund species by increasing the competitive ability of its best seedling but reduces coexistence when it makes the fecund species able to exclude its competitor.
Barabás and D'Andrea (2016)	Not specified	In two- and multispecies communities, heritable and and non-heritable ITV is added in a Lotka-Volterra-style model of ecological interactions.	Any trait	Individuals of a species vary along a unidimentional trait of interest. The distribution of a species' trait value at a given time is normal, with a total phenotypic variance that does not change in response to selection. Species' intraspecific standard deviations are uniformly sampled from four levels of variation: no variation, low, mixed and high levels of variation.	Negative except in some special cases.	The likelihood of coexistence is reduced by the presence of ITV except with mean-variance trade-offs. When ITV is heritable (allowing trait evolution), communities are more resilient to environmental disturbance.
Hart et al. (2016)	Plant communities	Non-spatial two-species model of annual plant competition in a spatially homogeneous context (Berverton-Holt model)	Response to competition (competitive sensitivity)	The response to competition is described by a symmetric, four-parameter beta distributions. There are four variance levels.	Negative	The concave-up relationship between competitive ability and seed production leads to non-linear averaging, disproportionately favouring species with low competitive sensitivity, leading to competitive exclusion.
Uriarte and Menge (2018)	Plant communities	Model from Hart et al. (2016) with introduction of spatial environmental structure using two patches in which each species has an advantage, connected by dispersal.	Response to competition	See Hart et al. (2016). IV can be the same across species and patches, or vary across species and/or patches. In this case, IV can be greater or smaller or the same in the preferred or non-preferred patch, and vary between species or not.	Variable	Spatial structure of IV matters. IV can facilitate local and regional coexistence thanks to non-linear averaging: The species that is on average the inferior competitor benefits more, as long as it specialises in the more fertile habitat. Greater IV in preferred habitat fosters coexistence and vice versa. Connectivity between patches must not be too large.

Study	Studied system	Model description	Trait on which IV is applied	Implementation of IV	Overall consequences of IV on coexistence	Detailed consequences of IV on coexistence
Banitz (2019)	Communities of sessile organisms	Individual-based competition model	Four life history traits (mortality rate, seed fitness, seed production rate, mean dispersal distance).	Two types of ITV: 1) unstructured, drawn in a truncated normal distribution centered on the mean species; 2) spatially structured (only for mortality and seed production rate), trait value is modified by a species-specific modification factor representing the species' response to the local environmental conditions. Seven scenarios test different configurations of these ITVs.	Variable or neutral	Unstructured IV does not impact coexistence while spatially structured IV increases coexistence only when response to the environment differs between species. This positive effect is due to a spatial storage effect. It is increased by equalising competition-colonisation trade-offs that don't involve dispersal distance while it is dampened by by spatially clumped disturbance, especially if there are interspecific trade-offs concerning dispersal distance.
Crawford et al. (2019)	Plant communities (grassland)	Individual-, trait-based, spatially explicit model. Plants are classified in PFTs. Only plants' resource uptake influences the amount of resources available in each cell a any time. Mortality is stochastic and influenced by the plant's resource stress and grazing, itself influenced by the plant's size.	Nine functional traits grouped in syndromes defining the plant's maximum size, its growth form, competitive ability and grazing response.	Individual trait values follow a truncated normal distribution centered around the mean trait's value. There are eleven different levels of ITV.	Variable	ITV increases the ability of the weakest species to invade most, but this effect does not scale to the community level and above a threshold ITV does not increase diversity further.
Mougi (2020)	Food webs	5-to 20 species eco-evolutionary community dynamics model based on a food-web model.	Growth and consumption rates	Intraspecific variability is heritable. 1 to 5 intraspecific genotypes parameters are sampled in a uniform distribution centered on general mean parameters, with a variance of 1.	Positive	Intraspecific variability favours evolution, which stabilizes the community, but only if it affects several species. This positive effect is weaker or even insignificant if IV affects only one trait.

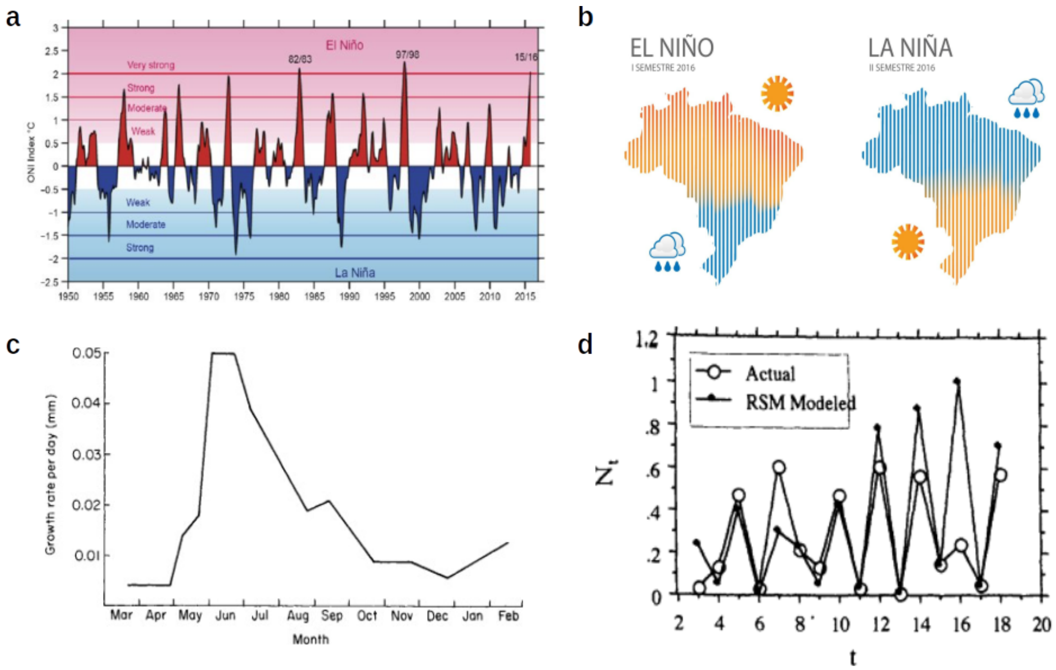

Figure 11: Examples of a temporally and spatially structured climatic phenomenon, and of temporally structured responses of plants. **a.** El Niño (red) and la Niña (blue) events in time. Copyright Hafez (2016). **b.** Spatial structure of the climatic effect of El Niño / la Niña in Brazil Copyright Bioagencia (`http://www.bioagencia.com.br/noticias/7911/la-nina-chegou-ao-fim-e-el-nino-pode-voltar-ainda-em-2017.html`). **c.** Average daily growth rate of Parmelia caperata. Copyright Hale (1970). **d.** Acorn production (kg/tree). Copyright Sakai (2001).

III. Intraspecific variability as a signature of species response to a multidimensional environment

III.1. Structure of intraspecific variability and species differences

In most of the cases shown above, intraspecific variability is treated as a random noise without any structure in space and time. However, it remains unclear if this is the case in the data from the field.

Indeed, both sources of intraspecific variability (genetic and environmental, see above) can be structured in space and time (Moran et al. 2016). Indeed, processes such as limited dispersal (Seidler and Plotkin 2006; Wiegand et al. 2021) and local adaptation (Schmitt et al. 2021) can lead to a spatial structure in the genetic composition of a population (Moran et al. 2016). In parallel, most environmental variables are structured in space and time. In time, they can be structured at several scales, for instance at the year scale (*e.g.* wet *vs.* dry years), at the seasonal scale (hot and cold seasons in temperate regions and wet and dry seasons in tropical regions) and across years (*e.g.* La Niña / El Niño events). In space, they can also be structured at different scales, from finer than the individual tree scale to longitudinal or altitudinal gradients. For instance, water availability, topography, light, microclimate and soil nutrient concentration and microorganisms show spatial structures (Tilman 1982 p. 101, Tymen et al. 2017; Kupers et al. 2019; Zellweger et al. 2019; Zinger et al. 2019).

The micro-environment in which an individual is as well as its past environmental conditions can influence its attributes, as is easily figured for growth in response to resource availability. These structured sources of variability necessarily lead to a structure in individual attributes. Recognising that intraspecific variability is structured radically changes the consequences for species coexistence. Whether it's because individuals are locally submitted to the same environmental conditions or because they have a similar genetic material, conspecifics can be locally similar although a high intraspecific variability is observed in the community. This structured variation would not be well represented by a random noise, which necessarily makes heterospecific individuals behave more similarly. Therefore, misattributing structured variation to stochasticity in models could have consequences on community dynamics (Moran et al. 2016). However, these consequences remain under-investigated.

III.2. Clark 2010, a pioneer (but often misunderstood) paper

In a seminal paper (almost 400 citations on Google Scholar in a decade), using a temperate forest dataset from southeastern U.S.A., Clark (2010) showed that although individuals within species apparently differ greatly in their performances (Figure 8c), conspecifics still respond more similarly to environmental variation than heterospecifics. He thereupon hypothesised that a large part of observed intraspecific variation was merely the reflection of species response to high dimensional environmental variation. In doing so, he did not present intraspecific variation as a coexistence mechanism *per se*, but rather proposed that species differentiation in many niche dimensions coupled with environmental variation in many dimensions enables stable species coexistence. Indeed, observed intraspecific variability is not interpreted here as a random (neutral) mechanism making species differences less pronounced, but as the result of the lack of knowledge due i) the mischaracterisation of variation in many biotic and abiotic environmental axes ii) the mischaracterisation of the response of species to these many niche axes. Accordingly, this paper falls within the niche theory (see the paragraph on the Hutchinsonian niche).

Yet, Clark (2010) along with other pieces of work (Clark et al. 2010, 2007) is often cited as a study showing a positive effect of intraspecific variability on species coexistence (*e.g.* Hart et al. 2016; Uriarte and Menge 2018; Westerband et al. 2021). This corpus has further been classified outside of niche theory, as "individual variation theory", which would explicitly identify intraspecific variation as the main driver of local diversity (Violle et al. 2012; Bastias et al. 2017; Crawford et al. 2019; Westerband et al. 2021). While this theory exists, it could be rather related to the "niche variation theory" (Van Valen 1965 in Bolnick et al. 2003). This altogether shows that Clark and colleagues' papers have been misunderstood, for instance by confusing the effect of individual random effects on model dynamics (Clark et al. 2007) and the effect of intraspecific variability observed in the field on species coexistence. Indeed, Clark and colleagues proposed to indirectly alleviate the effects of the lack of knowledge about environmental variation and species responses by using random individual and temporal effects that contributed to stabilise coexistence in models (Clark et al. 2007).

However, some other studies put this corpus back in the context of niche multidimensionality (*e.g.* Le Bec et al. 2015; Banitz 2019; Stump et al. 2022). Particularly, Stump et al. (2022) provide a clear summary of the core concept of Clark (2010). Indeed, they understood that the paper "argued that species coexist via high-dimensional niches, and proposed a test that used variability in growth and reproduction between individuals to detect such species-level differences", and that the individual level "reveal species-level differences in the response to environmental variation."

In this thesis, we propose to deepen the understanding and to fill several knowledge gaps about the intertwined concepts of high-dimensional coexistence and of observed intraspecific variability. Indeed, while Clark (2010)'s analysis focuses on temporal correlations, an analysis on variation in space is lacking. Similarly, this analysis has only been performed once using temperate forest datasets with a limited number of coexisting species, and never using tropical forest datasets with several hundreds of coexisting species. Moreover, an explicit test of the effect of the structure of intraspecific variability in community dynamics is lacking. Besides, while Clark (2010) hypotheses that the structure of individual correlations affects species coexistence, a clear demonstration is still needed. Finally, this structure of individual correlations could be a potential approach to enable species coexistence in community dynamics models when information on environmental variation and species responses is lacking (similarly to the use of individual random effects presented above). However, this approach remains unexplored.

III.3. Structure of the thesis

In this thesis, a combination of data analyses and modelling experiments is used to further explore the nature and structure of intraspecific variability, and its consequences on species coexistence. As a follow-up of Clark and colleague's approach, the role of high dimensional environmental variation and of species response to this variation in shaping intraspecific variability is further tested and discussed, to propose a renewed link between observed intraspecific variability and the ecological niche point of view of coexistence theory.

More specifically, in a first chapter, we clearly illustrate how intraspecific variability can arise from environmental variations in many dimensions that are imperfectly characterised, and not necessarily from genetic variations between individuals of the same species. We additionally test if intraspecific variability in growth can be observed even within clones, which would suggest that other fine-scale processes trigger variability. We then combine empirical evidence to test if intraspecific variability in growth is structured in space and if similarity among conspecific individuals is higher than among heterospecific individuals in tropical forests. We furthermore illustrate how this structure could arise from imperfectly characterised environmental variations and argue that this structure is often not well accounted for in most community dynamics models.

In a second chapter, using a simple community dynamics model, we test explicitly the effect of the way intraspecific variability is introduced in community models on the composition of the simulated communities, including the number of coexisting species. In doing so we explore if simple random distributions are a good proxy for intraspecific variability that is structured due to environmental variation.

In a third and final chapter, using a simulation approach as well, we test if similar response to environmental variations among conspecifics leads to species coexistence. We also investigate if environmental variation in high-dimension, which would allow each species to outperform the others in a given environment, is an additional necessary condition for species coexistence. We relate species coexistence to the higher correlation of performance in time within conspecifics and we further test if species-specific responses to high-dimensional environmental variation could be represented by a covariance structure in individual responses. We finally propose a novel approach for modelling community dynamics in a more realistic way when the environment is partially known (which is always the case), notably allowing for coexistence of a high number of species.

We finally discuss our approaches and provide perspectives for additional tests on the structure of intraspecific variability and for its integration in community dynamics models. Overall, we hope to trigger a renewed way to consider and represent intraspecific variability in community ecology.

Chapter 1

Rethinking the nature of intraspecific variability and its consequences on species coexistence

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Contribution to the chapter

I conceived the initial ideas together with Isabelle Maréchaux and Ghislain Vieilledent. This chapter led to the first contribution of the INTRACO working group, which the three of us initiated and coordinated. All authors contributed to the final study design and ideas within this working group. I led all the analyses, and I wrote the first draft of the manuscript together with Isabelle Maréchaux and Ghislain Vieilledent. All authors finally contributed to revisions.

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Chapter outline

Intraspecific variability has recently been seen as a potential lever to move forward in the understanding of the coexistence paradox – the fact that many species competing for the same resources are able to coexist. Intraspecific variability has therefore been included in theoretical community dynamics models aiming at testing its effect on coexistence. In most studies, it has been represented as a random noise unstructured in space or time. In this first chapter, we use complementary approaches that range from the theoretical illustration to the clonal dataset analysis to tropical forest inventories analyses to explore the nature and the structure of intraspecific variability. By proposing a renewed link between intraspecific variability and the classical framework of the high-dimensional ecological niche, we invite to rethink the role of intraspecific variability in species coexistence.

Abstract

Intraspecific variability (IV) has been proposed to explain species coexistence in diverse communities. Assuming, sometimes implicitly, that conspecific individuals can perform differently in the same environment and that IV increases niche overlap, previous studies have found contrasting results regarding the effect of IV on species coexistence. We aim at showing that the large IV observed in data does not mean that conspecific individuals are necessarily different in their response to the environment and that the role of high-dimensional environmental variation in determining IV has largely remained unexplored in forest plant communities. We first used a simulation experiment where an individual attribute is derived from a high-dimensional model, representing "perfect knowledge" of individual response to the environment, to illustrate how large observed IV can result from "imperfect knowledge" of the environment. Second, using growth data from clonal Eucalyptus plantations in Brazil, we estimated a major contribution of the environment in determining individual growth. Third, using tree growth data from long-term tropical forest inventories in French Guiana, Panama and India, we showed that tree growth in tropical forests is structured spatially and that despite a large observed IV at the population level, conspecific individuals perform more similarly locally than compared with heterospecific individuals. As the number of environmental dimensions that are well quantified at fine scale is generally lower than the actual number of dimensions influencing individual attributes, a great part of observed IV might be represented as random variation across individuals when in fact it is environmentally driven. This misrepresentation has important consequences for inference about community dynamics. We emphasize that observed IV does not necessarily impact species coexistence *per se* but can reveal species response to high-dimensional environment, which is consistent with niche theory and the observation of the many differences between species in nature.

Keywords — competition, environmental variation, high-dimensional niche, individual variation; intraspecific variability, spatial autocorrelation, spatial heterogeneity, species coexistence.

I. Introduction

Ecological communities are characterized by numerous coexisting species, for instance in grasslands, coral reefs or tropical forests. Understanding how these species stably coexist while competing for the same basic resources, *viz.* light, water, and nutrients (Baraloto et al. 2010), is a long-standing question in ecology (Gause 1934; Hutchinson 1961; Levine et al. 2017). Although numerous mechanisms have been suggested to contribute to species coexistence (Janzen 1970; Connell 1971; Chesson 2000b; Hubbell 2001; Wright 2002; Levine and HilleRisLambers 2009), it is unclear when and to what extent they explain the high species diversity observed in nature (Clark 2010). This is especially true in forests, where tree species coexist while seemingly requiring similar resources in the same location. Astonishingly, a hectare of tropical forest can harbor more than 900 plant species of a diversity of forms and functions (Wilson et al. 2012). Many theoretical mechanisms that might explain tree species coexistence were explored using the underlying assumption, explicit or not, that all conspecific individuals are identical (*e.g.* Lotka (1925) and Volterra (1926)'s competition models, Tilman's R*, Pacala et al. 1996, Rees 2001). However, intraspecific variability (IV) in traits, demographic rates or any proxy of performance, henceforth denoted as "attributes", can alter community structure and dynamics (Bolnick et al. 2011a). Indeed, large IV has been observed across a number of attributes in plant communities (Albert et al. 2012; Violle et al. 2012). For instance, Siefert et al. (2015) estimated that IV accounted for 25% of the variability in functional traits within plant communities on average, and this proportion was even estimated at 44% in a tropical forest (Poorter et al. 2018). Likewise, IV in growth rates for trees of standardized size, local crowding, terrain slope and annual effect has been found to account for up to 38% of total growth variability in a tropical forest stand (Le Bec et al. 2015).

IV, as a pathway for coexistence, has so far not shared the same attention as other mechanisms. This is in part because modeling studies that have explored the effect of IV on species coexistence have yielded contrasting results (Stump et al. 2022). In most theoretical analyses, variability in attributes among conspecific individuals has been included through independent random draws (Lichstein et al. 2007; Hart et al. 2016; Barabás and D'Andrea 2016; Crawford et al. 2019, but see Purves and Vanderwel 2014; Banitz 2019). Similarly, empirical studies typically summarize IV as a variance around species mean attributes (Jung et al. 2010; Albert et al. 2010; Siefert et al. 2015; Poorter et al. 2018). With this representation, IV can increase species niche overlap, thus making species functionally less different (*i.e.* "blurring species differences", Lichstein et al. 2007; Hart et al. 2016), sometimes slowing down competitive exclusion in models of community dynamics (Vieilledent et al. 2010; Crawford et al. 2019). However, in some other models, non-linear responses can make such IV beneficial to the superior competitors (*i.e.* the most competitive individuals of the more competitive species), thus accelerating competitive exclusion (*e.g.* Courbaud et al. 2012; Hart et al. 2016). Alternatively, in specific spatial configurations, more precisely when IV is greater in species preferred habitats, it has been shown to foster species coexistence (Uriarte and Menge 2018). Stump et al. (2022) have proposed to reconcile these contrasting results by distinguishing the effect of IV on niche traits (which control individual performance response to environmental conditions) *vs.* hierarchical traits (which control individual performance independently from environmental conditions). They demonstrated with different simulation models of community dynamics that IV in traits can alter stabilizing mechanisms and fitness differences in a complex way which depends upon the nature of the traits (niche *vs.* hierarchical) and their response curve, and thus promote or not species coexistence. In all the above examples however, IV, since simulated through independent random draws around species mean attributes, would be caused by differences among individuals that are fully independent of the environment: differences among individuals would remain unchanged even when experiencing exactly the same environmental conditions. Importantly, such simulated IV thus leads to a variation among conspecific individuals that is completely unstructured in space and time. New appreciation of fine-scale environmental heterogeneity and structure as well as species differences in their response to the environment, however, may suggest that this assumption of unstructured IV is rarely met. Novel remote sensing tools such as high-spatial and -temporal resolution airborne LiDAR scans (Tymen et al. 2017; Cushman et al. 2022), intensive soil samplings and metabarcoding (Zinger et al. 2019), and more generally studies on the microclimate (Zellweger et al. 2019) and microhabitats (Baraloto and Couteron 2010) have indeed evidenced strong environmental variation operating at fine scales (*e.g.* cm to meter scales) in many dimensions (Fig. 12). These environmental dimensions can be resources for which species compete (*e.g.* light, water, nutrients) but also all other components that shape the environment locally in space and time (*e.g.* temperature, wind, elevation, slope, soil texture, soil microorganisms *etc.*). In parallel, naturalists and taxonomists have long documented species differences in many aspects of their morphology and life history (Fig. 13). Such differences between species have then been specified and quantified through traits that drive each species response to the environment (species functional traits, (McGill et al. 2006; Westoby and Wright 2006). Similar to the environment that presents highly-dimensional variation at local scales, these functional species differences spread along many dimensions within communities (Hutchinson 1957, 1959; Baraloto et al. 2010; Kraft et al. 2015; Rüger et al. 2018; Maréchaux et al. 2020; Vleminckx et al. 2021).

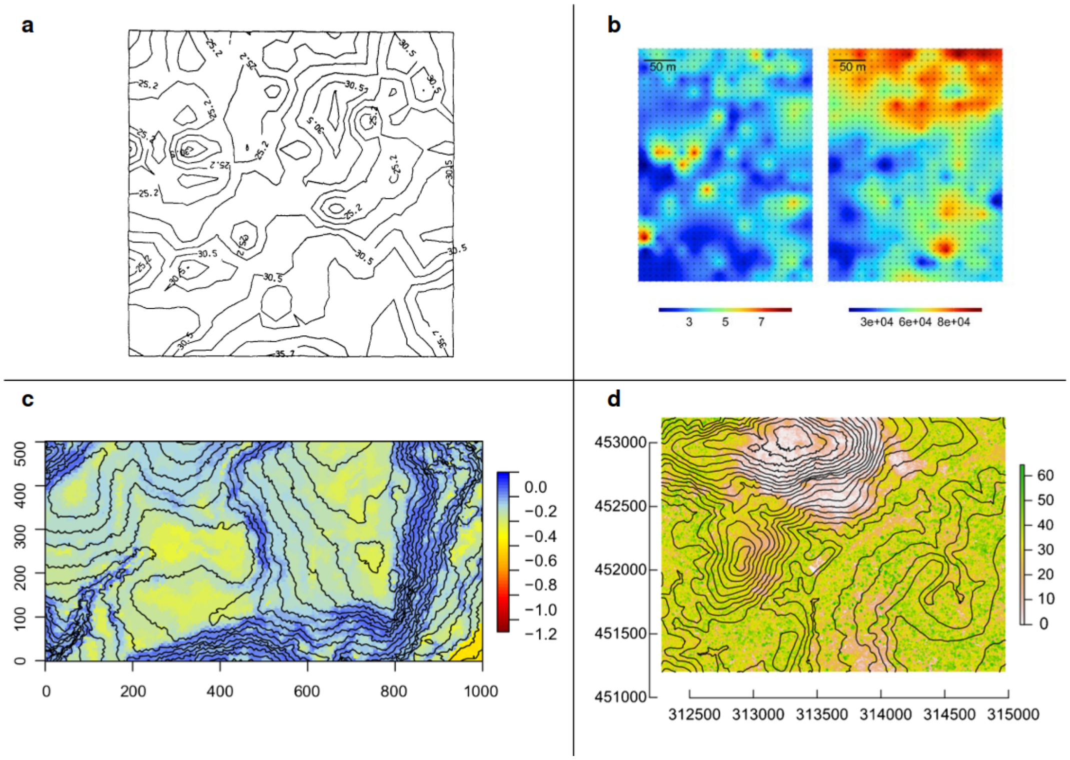

Figure 12: High environmental variability at a small spatial scale. **a.** Soil nitrogen content in a 12 × 12 m plot at Cedar Creek (USA) in g kg^{-1}. Copyright Tilman (1982). **b.** Carbon in % (left) and aluminum in ppm (right) soil content in a 12-ha (250 × 500 m) plot at The Nouragues (French Guiana). Copyright Zinger et al. (2019). **c.** Soil water content during mid-dry season of a regular year in MPa in a 50-ha (1000 × 500 m) forest plot at Barro Colorado Island (Panama). Coordinates in m. Copyright Kupers et al. (2019). **d.** Canopy height in m and topography (10 m spaced elevation lines) in a 50-ha (2500 × 2000 m) area at the Nouragues. Coordinates in m (UTM 22N). Copyright Tymen et al. (2017).

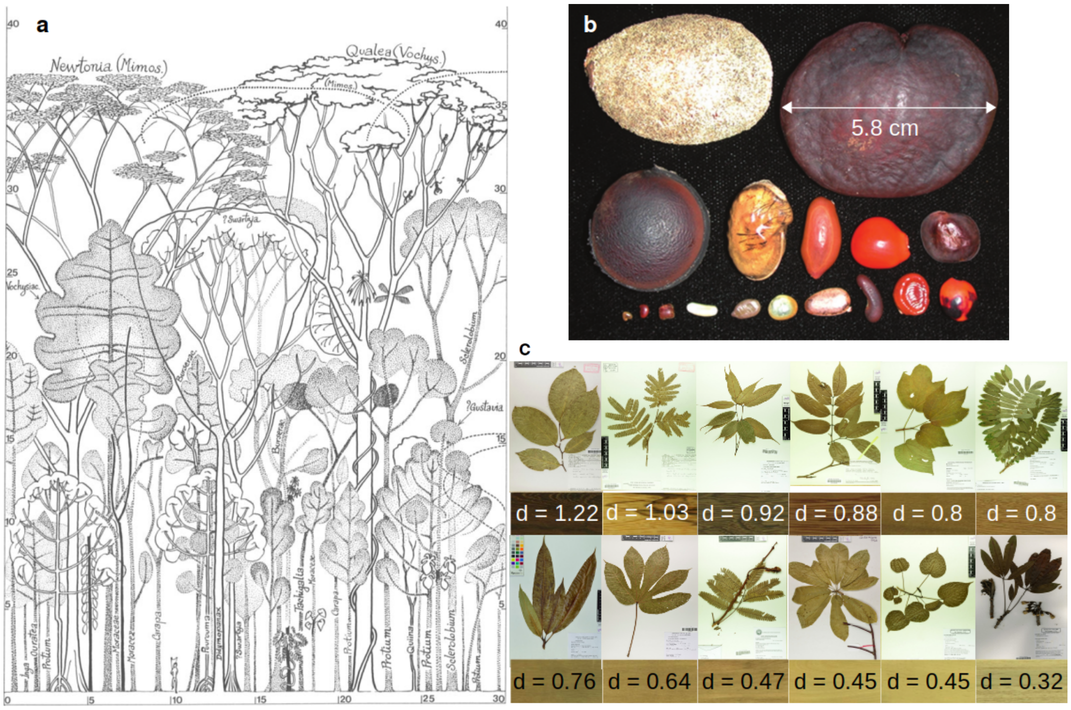

Figure 13: Morphological diversity of tree species illustrating strong differences between species. **a.** Diversity of tree species architecture and height in a tropical forest. Coordinates are in m. Copyright Hallé et al. (1978). **b.** Diversity of seed size and shape from 17 tree species of the Fabaceae family in the Peruvian Amazon. Copyright Muller-Landau (2003). **c.** Diversity of leaf size and shape (herbarium of Cayenne) and of wood aspect (reflecting wood characteristics) and density (CIRAD's xylotheque) for 12 tree species in French Guiana. Species from top left to bottom right are *Bocoa prouacensis*, *Zygia racemosa*, *Vouacapoua americana*, *Eperua falcata*, *Bagassa guianensis*, *Hymenolobium excelsum*, *Mangifera indica*, *Sterculia pruriens*, *Parkia nitida*, *Couroupita guianensis*, *Hura crepitans*, and *Ceiba pentandra*. Black bars next to herbarium samples indicate the scale (10 cm). Copyrights Gonzalez et al. (2021) and Normand et al. (2017).

In this paper, we explore the potential that the role of environmental variation in shaping observed IV has been largely underexplored with important consequences on our understanding of the effect of observed IV on community dynamics. Indeed, a great part of observed IV might emerge from species responses to a high-dimensional environment (Fig. 14): observed differences among individuals of the same species can be caused by the often poorly quantified response to the micro-environment they experience. This imperfect description can notably result from an insufficient set of environmental variables being measured, from a mismatch between the spatio-temporal scale of measurements and the one of individual attribute variation, or from measurement errors in both environmental variables and individual attributes. Apart from the latter, which can be unstructured and accounted for through specific tools (*e.g.* Calder et al. 2003), and that we do not explore here, the resulting variation among conspecific individuals would be structured in space and time, and not necessarily caused by genetic variation.The study is divided into three parts. In the first part, we present a virtual experiment to illustrate the fact that large observed IV can emerge from environmental variation, having thus consequences on the structure of IV. In the second and third parts, we present insights from experimental clonal Eucalyptus plantations and tropical forest inventories in order to test if these results are supported by experimental and empirical data. For each of these three parts, we detail the corresponding material and methods as well as the results. We then provide a general discussion. Throughout the study, we examine three main hypotheses (Fig. 15): (i) the large IV observed in natural communities can emerge from heterogeneity in multiple unobserved environmental dimensions which is often mischaracterized; (ii) because environmental variation is structured in space and time, IV is likely to be similarly structured as well, suggesting that it is not appropriate to represent IV as a purely random noise in models; and (iii) since a large observed IV does not necessarily imply that conspecific individuals substantially differ in their fundamental niche, conspecific individuals may still respond more similarly to environment than heterospecific individuals. We therefore call for a reconsideration of the nature and structure of IV, which could shed new light on the coexistence conundrum. While we acknowledge the existence of genetically-based individual variations, and that plasticity has a genetic basis (Nicotra et al. 2010; Westerband et al. 2021), we suggest that a substantial part of observed IV might result from the higher dimensionality of the species niche and the finer scale of environmental variation than typically observed. Species differences along these many dimensions can lead to multiple local inversions of species hierarchy in an environment varying in space and time, thereby allowing the stable coexistence of numerous species.

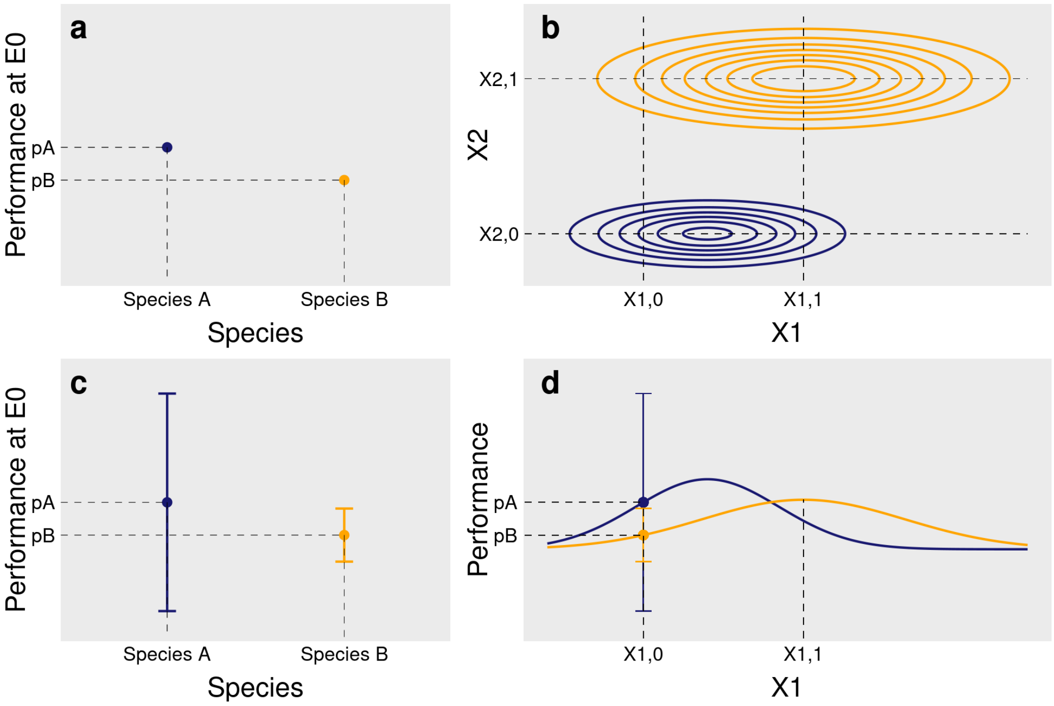

Figure 14: Reinterpreting observed intraspecific variability (IV): from niche widening to niche projection into a high-dimensional environment. In **a.**, within a given environment $E0$ defined along an environmental axis $X1$ ($E0 = E(X1, 0)$), conspecific individuals are identical and have the same performance pA and pB, for species A (blue) and species B (orange). Species A outcompetes species B in $E0$. Actual measured differences among conspecific individuals, shown in **c.**, can be interpreted in different ways. First, as conspecific individuals exhibit contrasting attributes in $E0$, they become more different. This can result in some heterospecific individuals having similar performances: IV would make species less different. Alternatively, IV measured in $E0$ results from the variation of unobserved environmental variables ($E0 = E(X1, 0, X2)$; **b.**). Contrasting performances among conspecific individuals in $E0$ do not result from intrinsic differences among them but from differences in the local environment they experience and that was poorly characterized, *i.e.* the number of observed dimensions is lower than the actual number of environmental dimensions. Similarly, although species niches present some overlap when projected on one dimension **d.**, they do not overlap in the two-dimensional space **b.**. Moreover, while species A outcompetes species B on average when $X1 = X1, 0$, the opposite occurs when $X1 = X1, 1$ **d.**, leading to an inversion of species hierarchy between different environments. Similarly, while species A outcompetes species B in $E(X1, 0, X2, 0)$, the opposite occurs in $E(X1, 0, X2, 1)$. Although only two dimensions are shown, species respond to many environmental variables varying in space and time, multiplying the possibilities of niche segregation and hierarchy inversions between species, offering room for species coexistence in a variable high-dimensional environment. The code used to generate this figure is available online.

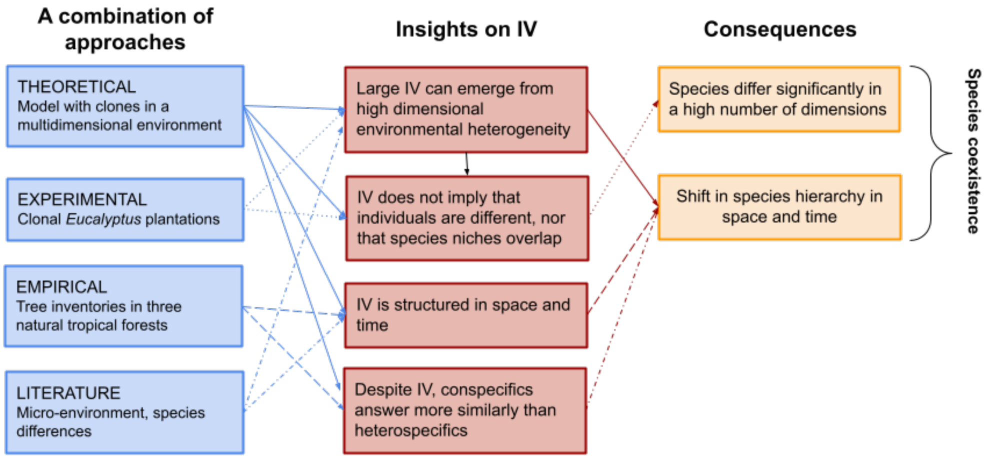

Figure 15: Multiple insights on the nature of IV and its consequences on individual and species differences. We used literature and data analyses of various nature to support the hypothesis that a large part of observed IV can result from multidimensional environmental variations that are spatially and temporally structured rather than by intrinsic and spatio-temporally unstructured differences between conspecific individuals, with radically different consequences on species coexistence.

II. Theoretical illustration: unobserved environmental dimensions result in large observed IV

We first conducted a virtual experiment to illustrate the hypotheses explored in this study. To do so, we generated simulated data of an individual attribute (*e.g.* tree growth) depending on a certain number of environmental variables varying in space, and then analyzed the simulated data assuming that most of the environmental variables are actually unobserved, as is typically the case in the field. This simulation experiment does not aim to accurately represent ecological reality, but to simply illustrate our points.

II.1. A “perfect knowledge” simulation model

We considered a set of J species with I individuals each, distributed in a virtual landscape. The environment was assumed to be fully known and defined by N environmental variables, X_1 to X_N, that were each randomly and independently generated in the landscape, assuming spatial autocorrelation. These variables could also represent the independent axes that would result from *e.g.* a PCA of many environmental variables. Individual location was drawn randomly in a virtual landscape defined by a $C \times C$ square grid, each cell corresponding to a particular environment (Fig. 16a). Individuals were identical within species (same model parameters for all conspecific individuals), but different between species (different model parameters between heterospecific individuals).

We considered the following “perfect knowledge” mathematical model, which depicts the exact attribute Y_{ijt} (*e.g.*, growth) of an individual i of species j given its environment at time t (Eq.1.1, Appendix 1).

$$ln(Y_{ijt}) = \beta_{0,j} + \beta_{1,j} ln(X_{1,ijt}) + \beta_{2,j} X_{2,ijt} + \cdots + \beta_{N,j} X_{N,ijt} \tag{Eq.1.1}$$

In this model, $\beta_j = [\beta_{0,j}, \ldots, \beta_{N,j}]$ is the vector of parameters defining the response of individuals of species j to the environment. Because conspecific individuals respond similarly to environmental variables, variation in Y_{ijt} among them is only due to differences in the environment where and when each individual is growing. Using this model, we computed the attribute Y of the $I \times J$ individuals at T dates, assuming that values for some of the environmental variables changed between dates, and thus obtained a simulated dataset $\{Y_{ijt}, X_{1,ijt}, \ldots, X_{N,ijt}\}$ with $N = 10$, $I = 300$, $J = 2$, $C = 500$ and $T = 2$.

II.2. An "imperfect knowledge" statistical model

Second, we considered an "imperfect knowledge" statistical model for which we assumed that only one explanatory variable X_1 (*e.g.*, light) in the above simulated dataset has been measured at the relevant scale among all the environmental drivers that actually determine response variable Y (Eq.1.2, Appendix 1). This model represents the ecologist's imperfect understanding of attribute Y, as few sites would actually offer quantification of variation of several environmental variables at the individual scale that is relevant. The model includes a species fixed effects on the intercept and on the slope ($\beta'_{0,j}$ and $\beta'_{1,j}$) and a random individual effect $b_{0,i}$ on the intercept with $b_{0,i} \sim \mathcal{N}(0, V_{bj})$, where V_{bj} is the intraspecific variance for species j. We estimated the model parameters based on the simulated dataset introduced above but considering only the first explanatory variable $\{Y_{ijt}, X1, ijt\}$, the remaining "unknown" environmental effects being contained in the model residuals, ϵ_{ijt}.

$$\begin{aligned} &ln(Y_{ijt}) = [\beta'_{0,j} + b_{0,i}] + \beta'_{1,j} ln(X_{1,ijt}) + \epsilon_{ijt} \\ &\epsilon_{ijt} \sim \mathcal{N}(0, V_j) \end{aligned} \tag{Eq.1.2}$$

We used default priors for variance parameters (Student's T with three degrees of freedom, location = 0 and scale = 2.5), and normal distributions (with mean=0 and variance=1) for mean parameters. The estimation of model parameters was done using a Bayesian approach using Stan software with the brms R package (Bürkner 2017, 2018). We used four MCMC chains with different initial values. We made 10,000 iterations for each chain with a warm-up period of 5,000 steps and a thinning rate of one fifth. We obtained 1,000 estimations per chain per parameter and examined trace plots, posterior distributions, R-hats and ESS statistics to check convergence of the chains (Appendix 1).

II.3. Apparent niche overlap and observed intraspecific variability as a result of unobserved environmental variables

Despite the fact that conspecific individuals were identical and species responses to environment were different, the variance estimates $\hat{V}_{bj}$ for individual random effects of species j were large, and species responses to the environment overlapped (Fig. 16b). This is due to the contribution of the unmeasured variables $\{X_{2,ijt}, \ldots, X_{N,ijt}\}$ in determining the variation of Y across individuals.

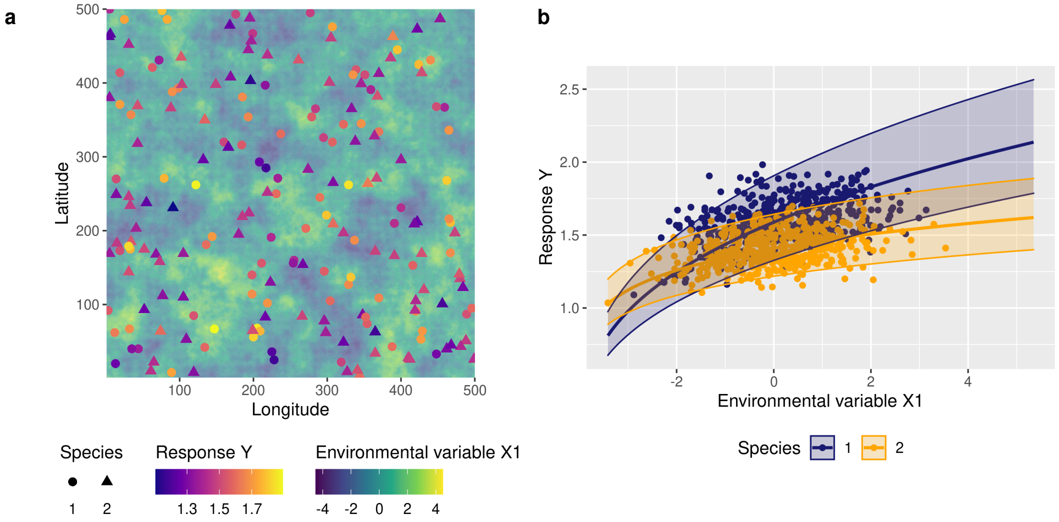

Figure 16: Observed intraspecific variability as a result of the imperfect characterization of the environment. A simulated response variable (Y, *e.g.* growth) is generated for individual clones of two species thriving in a high-dimensional environment. This response variable was first computed as a function of ten environmental variables ("perfect knowledge" model, Eq.1.1), but is then analyzed using a statistical model that accounts for the unique environmental variable that was assumed to be observed in the field (X_1, *e.g.* light) and includes a random individual effect ("imperfect knowledge" model, Eq.1.2). The intraspecific variability estimated with these random individual effects is then due to the variation in space and time of the nine unobserved environmental variables. **a.** Positions of a sample of $I = 600$ individuals from $J = 2$ species in a landscape defined by a square grid of $C \times C$ cells ($C = 500$). The background color indicates the value of the observed environmental variable X1 on each cell at date t. The response Y of each individual, which depends on the environment within each cell (Eq.1.1), is also indicated by a color scale. **b.** Response Y as a function of the observed environmental variable X_1 for the two species. Points represent the data $\{Y_{ijt}, X_{1,ijt}\}$. Thick lines represent the predictive posterior means for the two species. The envelopes delimited by two thin lines represent the 95% credible intervals of the predictive posterior marginalized over individuals (taking into account $\hat{V}_{bj}$). The envelopes thus represent the intraspecific variability which is due to the N-1 unobserved environmental variables.

Since it is driven by spatially autocorrelated variables (Eq.1.1), the response Y was spatially autocorrelated across conspecific individuals (Fig. 17). This means that two neighboring conspecific individuals have a more similar attribute Y than two distant conspecific individuals. Additionally, the variance of Y was lower within than between species: conspecific individuals responded more similarly to the environment than heterospecific individuals did (Fig. 17).

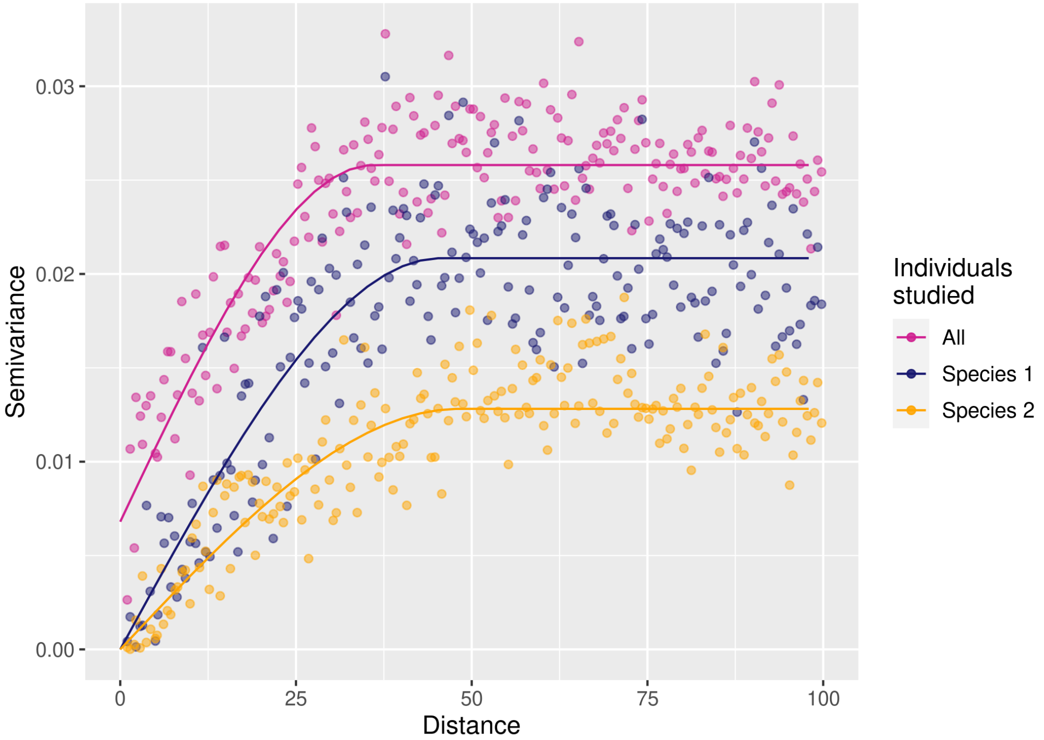

Figure 17: Spatial autocorrelation of attribute Y across individuals within and between species ($J = 2$) in a simulation experiment. This semivariogram represents the semivariance of the individual mean attribute Y as a function of the distance between individuals. The increasing curves evidence spatial autocorrelation in Y (similar results using Moran's I test). The semivariance of all individuals taken together (purple curve) is higher than the semivariance of conspecific individuals for the two species (orange and blue curves), which means that intraspecific variability is lower than interspecific variability.

With this simulation experiment, we simply illustrated that: (i) apparent high IV can emerge due entirely to an imperfect description of the environment exclusively, (*e.g.* unobserved environmental dimensions), (ii) the spatial structure of this IV follows the spatial structure of the underlying environmental variables, and (iii) this IV does not make species less different in their response to environmental variables (Fig. 17) despite apparent niche overlap in one dimension (Fig. 16b).

III. Experimental insights: large observed intraspecific variability in a clonal tree plantation

We then moved from a theoretical illustration to an experimental approach using census data from clonal Eucalyptus plantations, where genetic variability among individuals growing within a single same site is controlled. We explored the partitioning of IV between intrinsic (genotypes) and extrinsic sources, which is often infeasible in natural settings, to demonstrate that substantial observed IV can indeed emerge from genetically identical individuals in the field, even when persisting in an apparently homogeneous environment.

III.1. An extreme case of controlled genetic and environmental variation

The EUCFLUX experiment (São Paulo state, Brazil) is a clonal trial with a replicated, statistically-sound design (le Maire et al. 2019). It includes 14 genotypes of 5 different Eucalyptus species or hybrids of various origins. Each genotype is planted in plots of 100 trees, at a density of 1666 trees per hectare, and replicated spatially in 10 blocks (Fig. 18). The experimental set-up was designed to minimize the variation in environmental factors among blocks, which were separated by less than 1.5 km within a homogeneous 200-ha stand showing small variation in soil properties. Tree diameter at breast height (D) has been measured over 5 complete censuses, spanning 6 years, age at which such plantation is generally harvested (see le Maire et al. 2019 and Appendix 2 for further details on this experimental set-up).

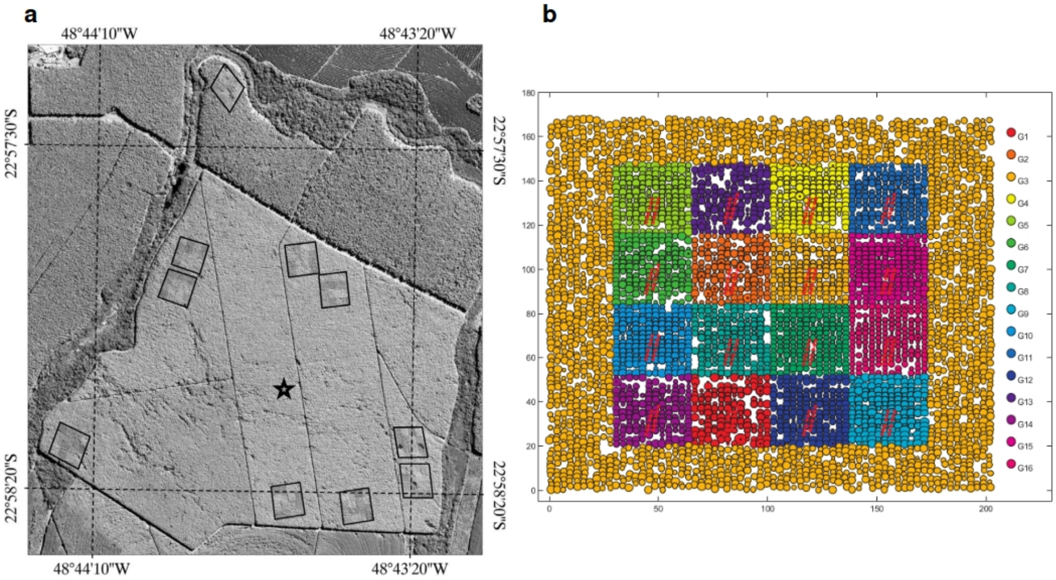

Figure 18: Experimental setup of the EUCFLUX experiment. The ten blocks **a.** and the organization of the 16 genotypes within a block **b.**. In our analyses, two genotypes were discarded because they were obtained from seeds and not clones and therefore included some genetic variability. A more complete figure legend can be found in le Maire et al. 2019.

III.2. A partitioning of observed variance among individual tree growth

We computed annual diameter growth (G) in mm yr^{-1} for each tree as well as a competition index (C) as the sum of the basal area of the eight direct neighbors of each tree. The dataset included 64,125 growth estimates corresponding to 13,531 trees in total. To quantify the relative importance of the different sources of growth variability, we used a statistical hierarchical growth model (Eq.1.3) including an intercept (β_0), fixed effects of the log-transformed diameter (β_1) and competition index (β_2), and random effects on the intercept for the block ($b_{0,b}$, with $b_{0,b} \sim \mathcal{N}(0, V_b)$), the genotype ($b_{0,g}$, with $b_{0,g} \sim \mathcal{N}(0, V_g)$), the census date ($b_{0,t}$, with $b_{0,t} \sim \mathcal{N}(0, V_t)$), and the individual ($b_{0,i}$, with $b_{0,i} \sim \mathcal{N}(0, V_i)$). All the data were log-transformed and scaled, and a constant of 1 mm was added to all growth values to avoid undefined logarithms.

Table 2: Mean posteriors of the Eucalyptus model and their estimation errors and residual variance partitioning among the different random effects.

	Intercept (β_0)	**Diameter** (β_1)	**Competition** (β_2)	**Individual variance** (V_i)	**Block variance** (V_b)	**Genetic variance** (V_g)	**Temporal variance** (V_t)	**Residual variance** (V)
Estimate	-3.50e-02	5.50e-01	-2.70e-01	2.30e-01	6.00e-02	1.30e-01	1.30E+00	5.10e-01
Estimation error	5.00e-01	5.00e-03	8.90e-03	4.00e-03	1.80e-02	3.10e-02	5.40e-01	2.00e-03
% unexplained variance				10.31%	2.69%	5.83%	58.30%	22.87%

$$\begin{aligned} &ln(G+1)_{it} = [\beta_0 + b_{0,b} + b_{0,g} + b_{0,t} + b_{0,i}] + \beta_1 ln(D)_{it} + \beta_2 ln(C)_{it} + \epsilon_{it} \\ &\epsilon_{it} \sim \mathcal{N}(0, V) \end{aligned} \qquad \text{(Eq.1.3)}$$

We used default Student's T priors for variance parameters, and normal distributions (with mean=0 and variance=1) for mean parameters. Model parameters were estimated using the same Bayesian approach as for the statistical model of the theoretical illustration (Appendix 2).

We then examined the proportion of the model residual variance (variation of the response variable that is not explained by the covariates) related to each random effect in order to partition the block, genotype, date and individual variances.

III.3. Variation among individuals is not explained by genotype

While minor variability was associated with blocks (Table 2), confirming that they are broadly homogeneous by design, the variability associated with temporal factors was predominant. This reveals that the competition index (C) used in the analysis to encapsulate the effect of progressive canopy closure does not fully encompass all temporal effects. Importantly, the variability between individuals was almost twice as high as the variability between genotypes (Table 2). Hence, even in such an extremely conservative case, where environmental variation in space is minimized and genotypic variability controlled, a large part of measured IV cannot be explained by purely-genetic differences among individuals that would remain independent of the environment as an IV simulated through independent random draws would be. This is in broad agreement with common garden studies in community genetics, which typically find a trait heritability lower than 1 for genetically-identical plants growing in a relatively homogeneous environment (*e.g.*, Shalizi and Isik 2019).

These results from a controlled experiment suggest an underestimated role of environmental micro-heterogeneity in shaping variation among individuals. This could be due to both unobserved environmental variables and a larger scale of environmental measurements (the plot) than the measured response (the individual scale). For instance inevitable spatial variation of biotic and abiotic variables (soil microbiome, pathogens, soil structure and water content, light, neighborhood interactions *etc.*) at fine scales (*e.g.* cm- to m-scale, hence impacting tree-scale environment, Baraloto and Couteron 2010, Fig. 12) as well as potential early manipulations of the young plant, the way it was planted, *etc.*, could drive individual growth response.

Table 3: Features of the three tropical forest data sets used as empirical case studies.

Site	**Rainfall** ($\mathrm{mm\,yr^{-1}}$)	**Sampling**	**Min DBH**	**Nb of censuses**	**Periodicity**	**Disturbance**	**Topography**	**Nb of species**	**Nb of individuals**	**Data source**
Paracou, French Guiana	3,000	15 × 6.25 ha (incl. 12 logged plots)	10 cm	24	1-2 y since 1992	Natural disturbances + selective logging	flat	613	69,548	Hérault and Piponiot 2018
BCI, Panama	2,600	50 ha	1 cm	8	5-y since 1980	Natural disturbances	hilly	225	37,224	Condit et al. 2019
Uppangala, India	5,100	5,92 ha (4 transects and 3 plots)	9.5 cm	20	1-yr since 1992	Natural disturbances	mountainous	102	3,789	Le Bec et al. 2015

IV. Empirical insights: observed intraspecific variability is high and spatially structured and does not "blur species differences" in tropical forests

To explore some of our hypotheses in natural communities, we then used data from three long-term tree inventories in tropical forests, from Amazonia (Paracou, French Guiana; Gourlet-Fleury et al. 2004)G, Central America (Barro Colorado Island, Panama; Losos and Leigh 2004) and South-East Asia (Uppangala, India; Pélissier et al. 2011). More specifically, we inferred observed IV, tested if individual growth showed local spatial autocorrelation, *i.e.* was structured in space, and if conspecific individual growth was more similar than heterospecific individual growth locally. These three sites encompass contrasting climatic conditions (rainfall ranging from 2,600 in BCI to 5,100 $\mathrm{mm\,yr^{-1}}$ in Uppangala), disturbance regimes (incl. various logging experiments in Paracou) and topography (from gentle in BCI to mountainous in Uppangala), making them representative of the global tropical forests. The data from these tropical forest inventories that we used in this paper are summarized in Table 3.

For all three datasets, annualized growth between two censuses was computed as the difference of DBH ($\geq$ 10 cm) between two consecutive censuses, divided by the time period between those two censuses. Growth estimates < -2 or > $\mathrm{mm\,yr^{-1}}$ as well as individuals from incompletely identified species and individuals and species with a single observation were discarded prior to analysis. Mean annual growth for each individual tree was then computed as the difference of DBH between the first and the last time a tree was measured, divided by the time period between those two measurements.

IV.1. High observed intraspecific variability in tree growth in tropical forests

To quantify the relative importance of intra- *vs.* interspecific variability in each site, we used a hierarchical growth model (Eq.1.4), including an intercept β_0, a diameter (D) fixed effect β_1,

Table 4: Mean posteriors of the tropical forest model and their estimation errors and residual variance partitioning among the different random effects.

	Intercept (β_0)	**Diameter (β_1)**	**Species variance (V_{bj})**	**Individual variance (V_{bi})**	**Residual variance (V)**
Paracou					
Estimate	2.30e-03	-2.30e-01	5.20e-01	5.50e-01	7.50e-01
Estimation error	2.30e-02	2.80e-03	1.70e-02	2.20e-03	5.70e-04
% unexplained variance			28.57%	30.22%	41.21%
Uppangala					
Estimate	8.20e-02	1.90e-01	3.70e-01	6.60e-01	5.90e-01
Estimation error	4.70e-02	1.30e-02	4.40e-02	8.60e-03	1.90e-03
% unexplained variance			22.84%	40.74%	36.42%
BCI					
Estimate	1.90e-01	-2.20e-02	6.70e-01	4.10e-01	8.10e-01
Estimation error	4.70e-02	4.50e-03	3.50e-02	4.10e-03	2.00e-03
% unexplained variance			35.45%	21.69%	42.86%

a species random effect $b_{0,j}$ (with $b_{0,j} \sim \mathcal{N}(0, V_b)$) and an individual random effect $b_{0,i}$ (with $b_{0,i} \sim \mathcal{N}(0, V_{bi})$) on the intercept. All data were log-transformed and scaled, and a constant of 2 mm was added to all growth values to avoid undefined logarithms.

$$\begin{aligned} &ln(G_{ijt} + 2) = [\beta_0 + b_{0,j} + b_{0,i}] + \beta_1 \times ln(D_{ijt}) + \epsilon_{ijt} \\ &\epsilon_{ijt} \sim \mathcal{N}(0, V) \end{aligned} \qquad \text{(Eq.1.4)}$$

We used default Student's T priors for variance parameters, and normal distributions (with mean=0 and variance=1) for mean parameters. We estimated the inter- and intraspecific growth variability from the variance of the species (V_{bj}) and individual (V_{bi}) random effects, respectively. Model parameters were estimated using the same Bayesian approach as before (Appendix 3). For the three sites, IV estimated from the growth model (V_{bi}, ranging from 0.41 to 0.66) was of the same order of magnitude as the interspecific variance (V_{bj}, ranging from 0.37 to 0.67) (Table 4). Overall, a large share of the variability in tree growth comes from individual effects in the three sites, even after accounting for the effect of diameter on tree growth, showing a high intraspecific variability in growth in these tropical forests.

IV.2. Spatial autocorrelation of individual growth within species at the local scale in tropical forests

To test whether individual growth was spatially autocorrelated, we performed in each site, spatial analyses of the mean individual growth values. We chose a conservative approach based on mean individual growth without accounting for the effect of diameter, thus without removing ontogenetic differences and considering the pattern of individual growth as it is in the field. More specifically,

Table 5: Spatial autocorrelation of the growth of conspecific individuals in three tropical forest sites. Shown are the proportion of species, and of corresponding individuals, in percent, for which individual growth among conspecific individuals is significantly positively spatially autocorrelated. The spatial autocorrelation of individual growth was tested using Moran's I index.

	Significant	**Not significant**
Paracou		
% Species	31.00	69.00
% Individuals	78.90	21.10
Uppangala		
% Species	18.50	81.50
% Individuals	45.30	54.70
BCI		
% Species	20.10	79.90
% Individuals	54.70	45.30

we performed Moran's I one-tailed tests as implemented in the ape R package (Paradis and Schliep 2019), for pairs of conspecific individuals less than 100 m apart in the same plot (to avoid capturing the effect of treatment in Paracou and including the spaces between the plots). For the most abundant species, we sampled 3,000 individuals with a uniform probability. We considered only the species with more than five conspecific neighbors less than 100 m-apart in the same plot. Positive spatial autocorrelation in tree growth between conspecific individuals was significant for 19 to 31% of the species in the three sites, representing between 45 and 79% of the total number of individuals (Table 5). Spatial autocorrelation was however much higher in logged plots as compared to unlogged in Paracou, because of a more heterogeneous light environment resulting from logging history (Appendix 3). Note that the absence of significant spatial autocorrelation for some species is partly explained by their low abundance (see Fig. 57 in Appendix 3).

Table 6: Comparison of local intra- and interspecific variability in individual growth for three tropical forest sites. The variability was estimated with the semivariance and the comparison was performed with a Mann-Whitney's test. The semivariances were computed for all species with more than five individuals and more than five heterospecific neighbors within 100 m in the same plot, and considering pairs of individuals that were less than 100 m apart and in the same plot. Shown are the proportion of species, and of corresponding individuals, for which **(i)** intraspecific variability was significantly lower than interspecific variability, **(ii)** intraspecific variability was significantly higher than interspecific variability, or **(iii)** the difference between inter- and intraspecific variabilities was not significant.

	Intraspecific variability $<$ Interspecific variability (i)	**Intraspecific variability $\sim$ Interspecific variability (ii)**	**Intraspecific variability $>$ Interspecific variability (iii)**
Paracou			
% Species	60.70	40.70	0.67
% Individuals	88.80	10.90	0.28
Uppangala			
% Species	42.20	62.20	4.44
% Individuals	57.70	23.60	18.80
BCI			
% Species	46.10	47.80	3.14
% Individuals	76.00	19.30	4.69

IV.3. Higher similarity of growth within conspecific than heterospecific individuals locally in tropical forests

To test if the performance of conspecific individuals was locally more similar than the performance of heterospecific individuals in the three sites, we also used mean individual growth, thus ignoring ontogenetic differences. We computed the mean individual growth semivariance (Baraloto and Couteron 2010) considering either conspecific or heterospecific neighbors within a 100-m radius. In the first case, semivariance was estimated as the mean of the squared difference in individual mean growth for all pairs of conspecific individuals. In the second case, semivariance was estimated as the mean of the squared difference in individual mean growth for all pairs of individuals with an individual of the focal species and one of another species. We considered only the species with more than five individuals, and with more than five heterospecific neighbors within the 100-m neighborhood distance. For each species, we then compared the semivariances between conspecific and heterospecific individuals using a Mann-Whitney test with a 0.05 alpha-risk. The mean individual growth semivariance appeared significantly higher among heterospecifics than among conspecific individuals for 42 to 61% of the species in the three sites, representing 58 to 89% of the total number of individuals (Table 6, see also Fig. 57 in Appendix 3 regarding species with non significant test). To control for a potential effect of species abundance on the semivariance estimations, we replicated the analysis by sampling a maximum of ten individuals per species. The results were qualitatively unchanged (Appendix 3).

With these results obtained with empirical data, we showed that i) observed intraspecific variability can be high in tropical forests, ii) individual growth can be spatially structured, and iii) conspecific individuals can have a more similar growth than heterospecific individuals at local scales. Altogether this suggests the signature of environmental variation that was not accounted for but that typically influences individuals at fine scale in many ways.

V. Discussion

V.1. High-dimensional environmental variation leads to large observed intraspecific variability

IV can result from intrinsic differences among individuals or from extrinsic environmental variation, including biotic factors, or interactions of both (Violle et al. 2012; Moran et al. 2016; Westerband et al. 2021). While much emphasis has been placed on genetically-driven IV in studies on coexistence (Booth and Grime 2003; Ehlers et al. 2016; Barabás and D'Andrea 2016), sometimes implicitly through the use of independent random draws across individuals (Lichstein et al. 2007; Hart et al. 2016; Crawford et al. 2019), and although we acknowledge its ecological and evolutionary importance, we here argue that the importance of environmentally-driven IV in natural communities has been underestimated and has radically different consequences for species differences and community assembly. More specifically, we argue that a large part of observed IV can result from an imperfect description of environmental variation in space and time.

First, using a simple simulation experiment, we illustrated how environmental variation in unobserved dimensions of the environment can produce large observed IV, although conspecific individuals are clones (Fig. 16). Similarly, the variance partitioning of individual tree growth within a common garden of Eucalyptus clones (le Maire et al. 2019) shows that the variance in growth between individuals is about twice as high as the variance between genotypes (Table 2). This reveals that a large part of the observed IV can emerge from non-genetic determinants, *e.g.* micro-environmental variations that are poorly characterized, even when the variation of the environment was sought to be minimized.

Importantly, because IV can emerge from environmental heterogeneity and without underlying genetic differences, observed IV does not necessarily imply that conspecific individuals substantially differ in their response to the environment, nor that species niches overlap (Fig. 14). Instead, large observed IV can also reflect the projection of species' high-dimensional niches within a high-dimensional environment that is variable in time and space: conspecific individuals differ with each other because they each thrive in a different micro-environment. In empirically observed data, such IV is therefore the result of projecting a high-dimensional response (*e.g.*, physiological processes), which is controlled by multiple macro- and micro-environmental variables, down to a low-dimensional, integrative response (*e.g.*, annual growth) that is poorly characterized because of an incomplete view of the environmental variables that contribute to it. This reassigns an important part of observed variation among individuals, often represented as neutral or random since they are seemingly unrelated to the observed dimensions of the environment (Fig. 14, Fig. 16, Table 2), to the classical niche theory (Hutchinson 1957) and is in agreement with natural history observations of individual trait differences that are associated to species-specific ecological strategies.

The "biodiversity paradox" highlights that a large number of species can coexist while competing for a limited number of resources (Hutchinson 1961). This puzzling question has generally been tackled considering trade-offs along a limited number of niche axes, often corresponding to resources (Tilman 1982; Rees 2001). But if the number of resources may indeed be relatively limited (*e.g.*, light, water, and nutrients for plants), the number of independent environmental factors (*e.g.* microclimatic variables) that drive the performance of individuals for a particular level of resources is not. Environments are known to vary along multiple dimensions at fine scales in space and time (Fig. 12), and in many cases, this variation has been shown to influence individual attributes (*e.g.*, Fortunel et al. 2020).

Nevertheless, despite technological advances, many of these abiotic and biotic environmental factors are still poorly understood and monitored. As a result, the dimensionality of field observations is typically low compared with the high dimensionality of the environment in nature and the scale of environmental measurements is often coarser than the scale of the actual environmental variation (Bramer et al. 2018; Estes et al. 2018). The variability in individual attributes due to the variation of environmental variables that is not characterized therefore remains mostly a black box, and is typically summarized in terms of residual variance in statistical models (Albert et al. 2012; Siefert et al. 2015) or encapsulated into so-called "individual random effects" (Clark et al. 2007). We here emphasize that even in the absence of any intrinsic differences among conspecific individuals, a large IV can emerge from the imperfect characterization of the environment (Fig. 14, Fig. 16, Table 2), which varies in a high number of dimensions at fine scales (Fig. 12).

V.2. Intraspecific variability is structured in space and time

IV has commonly been modeled through independent random draws around the species mean in community ecology studies (Lichstein et al. 2007; Courbaud et al. 2012; Hart et al. 2016; Barabás and D'Andrea 2016; Uriarte and Menge 2018). While this representation typically results from a lack of knowledge, with randomness being used as a substitute for more detailed understanding of underlying ecological processes (Clark et al. 2007), it encapsulates strong hypotheses relating to the nature of IV that are rarely discussed. In contrast, we emphasize here that IV is generally non-random and structured in both space and time.

At a given time, conspecific individuals that are distributed across space can strongly vary in their attributes (Violle et al. 2012; Siefert et al. 2015; Moran et al. 2016; Poorter et al. 2018). While this spatial IV has often been represented as random in community dynamics models, *i.e.* implying that conspecific individuals can perform differently within the same environment (Fig. 14c), a large part of this variability appeared in fact structured in space and likely associated with fine-scale spatial changes in the environment (Fig. 14b, Moran et al. 2016). In our illustrative simulation experiment, the attribute of conspecific individuals varies spatially as a result of the environmental variation in space, and the spatial autocorrelation of conspecific attributes reflects the spatial autocorrelation of the environmental variables (Fig. 16, Fig. 17). While in our illustrative example, the attribute could be any trait or proxy related to performance, in our data analyses, only growth was investigated. We hypothesize that the relationship between the investigated attribute and environmental variables drives the spatial autocorrelation due to environmental structure; thus so-called "response traits" (*i.e.* influenced by the environment, Lavorel and Garnier 2002) should show similar spatial patterns than the ones here observed with growth. Moreover, the more an attribute integrates multiple processes (as for growth), the more likely it is to be controlled by the environment, and therefore should have a structured spatial pattern. We further hypothesize that the more related to performance an attribute is, the more likely it is to show spatial patterns due to local adaptation. Determining which and how traits are related to performance remains one of the main research challenges of functional ecology (see *e.g.* Violle et al. 2007; Shipley et al. 2016; Brodribb 2017).

Similarly, data from three long-term forest inventory sites across the tropics revealed spatial autocorrelation in tree diameter growth of conspecific individuals (Table 4), the insignificance of spatial autocorrelation for some species being constrained by their low abundance (Appendix 3). These results suggest that IV is strongly driven by the spatial variation of the environment, which is itself highly structured (Fig. 12). However, we acknowledge that genetically-driven IV can also be spatially structured, for instance via dispersal patterns or natural selection (Moran et al. 2016). We hypothesize that in that case, attributes would likely be randomly structured in space (Getzin et al. 2014) or correlated at the spatial scale of seed dispersal, typically several tens of meters in tropical forests Clark et al. 2004; Seidler and Plotkin 2006; Muller-Landau et al. 2008, while environmental variables are typically highly spatially correlated at fine scales (*e.g.* meter scale, Baraloto and Couteron 2010). We also acknowledge that natural selection can happen at fine scales (Marrot et al. 2021), and could thus produce spatially structured IV due to local genetic adaptation. Nevertheless, data documenting genetic variation within species can still reveal higher similarity between conspecific than heterospecific individuals locally as well as non-overlapping species niches (Schmitt et al. 2021). Importantly, any local genetic adaptation does not preclude that the imperfect characterization of environmental variations generates large observed IV that is structured in space and time and whose consequences cannot be well represented and understood using a random variation around a species mean.

In communities of sessile organisms such as trees, IV has been commonly structured in space using individual random effects, which vary among conspecific individuals but stay constant through the lifetime of individuals (Clark et al. 2007; Vieilledent et al. 2010). We here argue that while this approach can reveal the spatial structure of IV through inference, the use of the resulting estimated standard deviation term to introduce individual variation in simulations of community dynamics is not sufficient to produce a spatially structured IV, as we showed is observed in natural communities. Similarly, individual attributes can change over time. Because individuals within a species can be measured at different points in time, as it is often the case when assembling functional trait databases for example (Zanne et al. 2009; Kattge et al. 2020; Albert et al. 2011), this can lead to observed IV with no observable structure when it is only characterized by a variance around a species mean (Fig. 14c). But a large part of this observed IV is actually structured in time and associated with temporal changes in the environment. For instance, the temporal storage effect (Chesson and Warner 1981), a well-known coexistence mechanism, structures species performance because species are able to “store” growth during favorable timespans to overcome lean times; mast-seeding or masting, which describes periodic and synchronized massive seed production of conspecific individuals, would also result in a temporally structured IV (Koenig and Knops 2005). Temporal variation in individual response within a species can typically be structured with temporal random effects (Clark et al. 2007). Temporal random effects have been used to estimate the inter-annual variability in tree growth Metcalf et al. 2009; Fortunel et al. 2018) and fecundity (Clark et al. 2007) for example. In all those examples, temporal environmental variation affects conspecific attributes in the same way (Clark 2010).

Overall, the representations of IV rarely reflect the overwhelming empirical observations that IV is spatio-temporally structured by the environment, ontogeny, local adaptation and interactions between those factors. We therefore call for a reconsideration of the nature and the way of integrating IV into models of community dynamics. When IV is modeled randomly with a variance around a species mean, it implies that conspecific individuals can perform differently in the exact same environment, thus implying intrinsic differences between conspecific individuals. This type of unstructured IV can result in an overestimated increase in species niche overlap, which makes species more similar in their response to the environment (Fig. 14a and c, Stump et al. 2022). While trait heritability has rarely been considered in studies on the role of IV on coexistence (but see Barabás and D’Andrea 2016), in some studies, the random variation in attributes across conspecific individuals is considered as environmental, because it is not heritable in the model (*e.g.* Lichstein et al. 2007; Moran et al. 2016). However, environmentally-driven IV should be structured in space and time, as the environment is (Fig. 12, Fig. 17). In addition, when

IV is randomly distributed among conspecific individuals, similarity among conspecific individuals is systematically underestimated, which is not the case when IV is structured in space and time (Purves and Vanderwel 2014; Banitz 2019), as discussed hereafter.

V.3. Conspecific individuals respond more similarly than heterospecific individuals locally

Species differ in multiple attributes, responding to a high number of environmental variables (Fig. 13), but often in ways that cannot be readily observed. If observed IV results mainly from high-dimensional environmental variation in space and time rather than from intrinsic differences between conspecific individuals, then for a given environment, conspecific individuals should respond more similarly than heterospecific individuals. This is the case in our illustrative simulation experiment, where the fact that conspecific individuals have exactly the same set of parameters and respond identically to spatial and temporal changes in the environment results in higher inter- than intraspecific variance in the response locally (Fig. 16, Fig. 17).

Corroborating this point of view, pairs of conspecific individuals in 11 North-American temperate forest stands showed higher correlation in their temporal variation of growth rate or fecundity than pairs of heterospecific individuals on average (Clark 2010). This indicates that conspecific individuals responded more similarly to environmental variation in time than individuals of different species. Importantly, these results were obtained in a system with high observed IV (leading to an apparent species niche overlap), where species responded in the same direction to environmental changes (*e.g.* increased tree growth in climatically favorable years). Hence, considering the temporal structure of IV revealed species differences that were not apparent otherwise, since they led to spreading along a high number of dimensions that varied at fine scales (Clark 2010). However, as well highlighted by Stump et al. (2022), these results were often misinterpreted as an evidence that IV fostered coexistence. As another piece of evidence presented here, pairs of spatially proximal conspecific individuals tended to present more similar temporal means in absolute tree growth than pairs of close heterospecific individuals across three large contrasted tropical forest sites (Table 6). This provides new empirical evidence that, although estimated IV can be substantial, conspecific individuals respond more similarly than heterospecific individuals to environmental variation in space.

A stronger similarity in the response to environment between conspecific than heterospecific individuals locally is the signature of differences in species response to the environment. As a result environmental variation in space and time leads to local or punctual inversions of species hierarchy in performance (Fig. 14d). As possibilities of hierarchy inversions between species increase rapidly with increasing dimensionality (Fig. 14b) and variability of the environment, the high-dimensionality of the environment offers room for the stable coexistence of numerous species (Falster et al. 2017; Rüger et al. 2018). In the end, we therefore argue that a substantial part of IV is not a mechanism for coexistence in itself but can rather be the signature of species differences and environmental variation that allow coexistence: the high-dimensional species differences, which make them respond differently in a high-dimensional environment varying in space and time, can only be observed at the individual scale. In the absence of precise information on the many dimensions across which species differ and environment varies, large observed IV is the evidence of the niche mechanisms enabling species coexistence.

V.4. Recommendations and concluding remarks

Most of the theoretical studies that have explored the role of IV in species coexistence so far did so by adding variances around species-specific means, thus considering IV as stochastic, which implies that conspecific individuals perform differently in the same environment. Here, we provide insights suggesting that large observed IV can emerge from environmental heterogeneity and is structured in space and time. We stress that this interpretation has strong consequences on the understanding of the effects of IV on species coexistence: (i) observed IV does not necessarily imply that conspecific individuals are strongly intrinsically different nor that species niches overlap, and (ii) the spatial and temporal structure of observed IV reveals stronger correlations of individual responses within species at local spatio-temporal scales, which reveals species niche differences in many dimensions. We thus call for a reconsideration of the nature of IV and of the way it is integrated in models, by thoroughly distinguishing its sources (intrinsic *vs.* extrinsic, and their interactions).

We acknowledge the existence of genetically-driven IV, potentially due to local adaptation to the microenvironment, and its eco-evolutionary importance, but suggest that multidimensional environmental variation generates a large observed IV that is structured in space and time. We underline that environmentally-driven structured IV has been largely overlooked in previous community ecology studies and has consequences on community dynamics which cannot be represented and understood using a random variation around a species mean. To this end, we recommend that empirical studies explore further the spatio-temporal structure of IV and how it relates to environmental variation along multiple dimensions, the differences in IV structure between species, and, when possible, assess the relative importance of genetically and environmentally driven IV, for instance by means of common garden experiments. Models of community dynamics should then endeavor to structure IV in space and time so that it reflects the high-dimensional variation in both the environment and species attributes, and not only some intrinsic differences between conspecific individuals (Purves and Vanderwel 2014; Moran et al. 2016; Banitz 2019). In both empirical studies and models, this implies that the species attributes are measured at the individual level, localized in space, and repeatedly observed in time. Adding spatio-temporal structure into the unexplained individual response in a community dynamics model will not properly substitute for the role of imperfectly characterized environmental variables however, particularly regarding the effect of environmental filtering. In particular, much care should be taken not to undermine the explanatory power of environmental variables in models when they are informed at a coarser scale than the individual scale, as it has been reported (Smart et al. 2021). Simultaneously, the monitoring of multiple environmental variables at fine scales in space and time is required in order to better capture their effect on individual attributes (such as physiological or mechanistic traits, Shipley et al. 2016; Brodribb 2017), hence reducing the part of unexplained IV, and ultimately to better characterize the high-dimensionality of species niches. Altogether, these recommendations will enable to better account for species differences that are expressed at the individual level and evidence their impacts on the community dynamics *in natura* and *in silico*.

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Supporting information and data access

The appendices and all the code used for this study are available in a GitHub repository (`https://github.com/camillegirardtercieux/coexIV`) and have been permanently archived on Zenodo (`https://doi.org/10.5281/zenodo.5504013`).

Appendix 1: Simulation experiment with two species.
Appendix 2: Analysis of an Eucalyptus clonal plantation dataset.
Appendix 3: Analysis of tropical forest inventory data.

No new data were used in this study. For access to forest plot inventory data and Eucalyptus plantation data used in this study, refer to the data used in Le Bec et al. 2015; Hérault and Piponiot 2018; Condit et al. 2019; le Maire et al. 2019. However, the analyses and reflections presented here are original.

Declaration of interests

All authors declare that they have no conflict of interest.

Chapter 2

Beyond variance: simple random distributions are not a good proxy for intraspecific variability in systems with environmental structure

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Contribution to the chapter

I conceived the initial ideas together with Isabelle Maréchaux and Ghislain Vieilledent. All authors contributed to the final study design and ideas within the INTRACO working group. I led all the analyses, and I wrote the first draft of the manuscript together with Isabelle Maréchaux and Ghislain Vieilledent. All authors finally contributed to revisions.

This chapter is in revision at PCI Ecology.

Chapter outline

As illustrated and discussed in Chapter 1, intraspecific variability can be structured in space and time, particularly when it originates from environmental variations. However, it is mostly represented using a random, unstructured probability distribution in theoretical community dynamics models which aim at testing the effect of intraspecific variability on species coexistence. In this second chapter, we provide a simulation experiment to test the effect of the way intraspecific variability is introduced in a community dynamics model.

Abstract

The role of intraspecific variability (IV) in shaping community dynamics has been intensively discussed over the past decade and modeling studies have played an important role in that respect. However, a major, but often implicit, assumption typically made by these studies, that IV can be represented by independent random draws around species-specific mean parameters, has largely remained undiscussed. A great part of observed IV is however structured in space or time, in particular when resulting from environmental dimensions that influence individual performance but are imperfectly characterized or unobserved in the field. To test this assumption, we designed a simulation experiment where we varied the level of knowledge of the environment in virtual communities, resulting in different relative importance of explained *vs.* unexplained individual variation in performance. We used a community dynamics simulator to generate communities where the unexplained individual variation is, or is not, added as an unstructured random noise. Communities simulated with unstructured IV never reached the community diversity and composition of those where all the variation is explained and structured (full knowledge model). This highlights that incorporating unstructured IV (*i.e.* a random noise) to account for unexplained (but structured) variation can be misleading. Also, comparing communities simulated with the same level of knowledge of the environment, but adding unstructured IV or not, we found that the effects of incorporating unstructured IV depended on the relative importance of structured versus unstructured IV. In particular, increasing the proportion of unstructured IV into the model moved from a positive to a negative effect on community diversity and similarity in composition with the full knowledge model. This suggests that it is crucial to account for the sources and structure of observed IV in real communities to better understand its effect on community assembly and properly include it in community dynamics models.

Keywords — community dynamics, community model, ecological niche, environmental filtering, high-dimensional environment, individual variation, species coexistence.

I. Introduction

The role of intraspecific variability (IV) in shaping community dynamics has been intensively discussed over the past decade (Bolnick et al. 2011a; Albert et al. 2011; Violle et al. 2012). Observed IV, *i.e.* the variability among measured individual attributes (functional or demographic traits, or any proxy of individual performance) within a species has indeed been reported to be large within communities (Siefert et al. 2015; Poorter et al. 2018). Modeling studies have played an important role to decipher the effect of IV on species coexistence (*e.g.* Lichstein et al. 2007; Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019), offering opportunities of virtual experiments out of the scope of empirical approaches. These studies have led to contrasting results however, letting the debate unresolved: IV could either (i) blur species differences, thus promoting transient or unstable coexistence (Vieilledent et al. 2010; Crawford et al. 2019), (ii) disproportionately advantage the strongest competitor, thus hindering coexistence (Courbaud et al. 2012; Hart et al. 2016), or (iii) promote coexistence in specific spatial configurations (Uriarte and Menge 2018). While a unifying framework differentiating whether IV affects niche traits or hierarchical traits has been recently proposed to explain these discrepancies (Stump et al. 2022), a major assumption usually made in modeling studies, namely that IV is unstructured in space or time and can be represented by independent random draws around species-specific mean parameters, remains largely undiscussed (Girard-Tercieux et al. 2023).

The IV observed on individual attributes can, however, emerge from various genetically- and environmentally-driven processes (Violle et al. 2012; Moran et al. 2016). Most of these processes are unlikely to generate unstructured IV in the form of a normal noise. Instead, IV can be highly structured in space or time. In particular, high-dimensional (and often unobserved) variation of the environment can lead to large observed IV. For instance, in a highly controlled clonal experiment, IV in tree growth within clones was larger than genetically-driven IV between clones (Girard-Tercieux et al. 2023). Differences in attributes among conspecific individuals can result from differences in unobserved environmental dimensions, and do not necessarily mean that conspecific individuals substantially differ in their response to the environment. While it is widely accepted that environmentally-driven structured IV (sIV) is ubiquitous in natural communities (Nicotra et al. 2010), the consequences of its substitution by unstructured IV (uIV) on species coexistence and community dynamics remain to be thoroughly tested in models (Clark 2010; Girard-Tercieux et al. 2023).

Here, we explore the effect of considering IV either as structured by environmental dimensions (sIV) or as an unstructured random noise (uIV), using a simulator of community dynamics. To do so, we created a virtual plant community, where individual performance is fully determined by species-level responses to 15 environmental dimensions (*Perfect knowledge model*, Fig. 19A). We then considered imperfect knowledge models, where this 15-dimensional individual performance is estimated using 0 to 15 supposedly "observed" environmental dimensions, while the remaining IV (or unexplained variation) resulting from effect of "unobserved" environmental dimensions, is ignored (*Imperfect knowledge models without uIV*) or is included as random unstructured IV (*Imperfect knowledge models with uIV*, Fig. 19B). These three performance models are used to run a community dynamics simulator and assess their effects on species coexistence and community dynamics.

Specifically, we are asking two questions: First, how well does random unstructured IV (uIV) mimic the effect of environmentally-driven structured IV (sIV) on diversity and community composition? To answer this question, we compare communities simulated under the *Perfect knowledge* *model* and under *Imperfect knowledge models with uIV*. These models share the same amount of total variation, but partitioned differently between sIV and uIV, depending on the amount of knowledge of the environment we consider (Fig. 19C, arrow 1). Second, how does the effect of adding uIV on diversity and community composition (Fig. 19C, arrow B) vary with the knowledge of the environment (Fig. 19C, arrow C), *i.e.* with the relative importance of sIV and uIV in our model? To answer this question, we compare pairs of models with the same amount of sIV, *i.e.* with the same knowledge of the environment, but including or excluding uIV. This latter comparison corresponds to the approaches proposed in previous studies testing the effects of IV on coexistence (Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016).

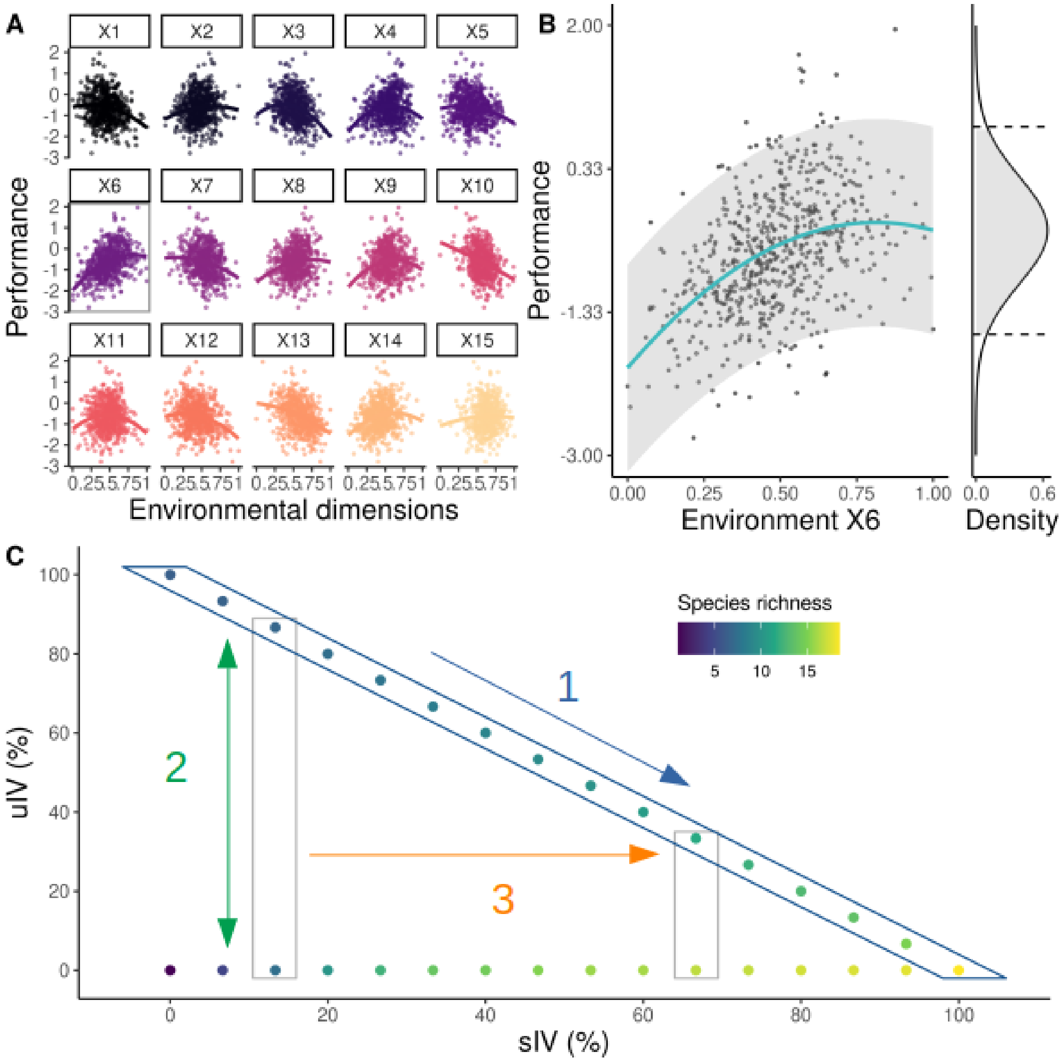

Figure 19: Conceptual framework. Consider an environment that is varying in many dimensions, X1 to X15. Each dimension influences individual performance in a species-specific way, as illustrated in A for one species. In practice, several of these environmental dimensions are actually unobserved in the field. The effect of unobserved environmental dimensions on individual performance results in an observed intraspecific variability (IV) in the species response to observed dimensions (*e.g.* X6 in B). This variability is often represented as a probability distribution, with individual random draws that are independent and unstructured in space and time (B). We propose a framework to assess the consequences of representing the variation resulting from unobserved environmental dimensions, which has an inherent structure, by such unstructured IV (uIV) on community dynamics, and how these consequences vary with the level of knowledge of the environment (C). To do so, we varied from 0 to 15 the number of dimensions that are observed and used for estimating the 15-dimensional performance. By increasing the number of observed dimensions, we thus increased the proportion of structured IV (sIV) that is accounted for in estimating individual performance (C, horizontal axis; see also Fig. 20). For a given number of observed dimensions, or % of sIV, the variation resulting from unobserved dimensions can be either added as uIV or not (C, vertical axis). For each way to estimate performance (with uIV or not, and with different numbers of observed dimensions), we simulated community dynamics using the same simulator. We then compared the simulated communities in terms of diversity and composition (*e.g.* species richness in colored points in C). By comparing communities simulated with uIV with the one with 100 % sIV (arrow 1) we tested the effect of substituting sIV with uIV on community dynamics. By comparing communities simulated with and without uIV, for a given % of sIV (arrow 2), we mimicked the approach of previous modeling studies testing the effect of intraspecific variability on community dynamics and species coexistence. By comparing this difference between communities simulated with and without uIV across different % of sIV (arrow 3), we tested whether the results of previous studies can be influenced by the level of knowledge of the environment.

II. Materials and methods

II.1. Environmental variables

We consider a grid of $25 \times 25 = 625$ sites. Each site i is characterized by a multidimensional environment defined by 15 environmental variables $x_1, \ldots, x_{15}$. Each environmental variable is spatially auto-correlated and independently derived from a conditional autoregressive model, with a normal distribution centered on 0 and of variance 1. Therefore, environmental variables are not uniformly distributed, some habitats ($x_1, \ldots, x_{15}$ values) being more frequent than others. Environmental variables are then scaled to $[0, 1]$.

II.2. Individual performance

We consider 20 species, whose individual performance is computed in three alternative ways, as follows.

II.2.a. The *Perfect knowledge model*

We first consider a simple model representing the "real" functioning of a plant community, *i.e.* where all determinants of individual performance are known. We consider that the environment is multidimensional and partitioned among species. To this end, in this *Perfect knowledge model*, the performance of individuals of species j is maximal at one point in the multidimensional environmental space, denoted $x_j^* = (x_{1,j}^*, \ldots, x_{15,j}^*)$. For an environmental axis k, $x_{k,j}^*$ is drawn in a uniform distribution in $[0, 1]$. Then, the performance of an individual of species j on site i, p_{ij}, is computed as the additive inverse of the normalized Euclidean distance between x_j^* and the local environment at the site where the individual thrives, $x_i = (x_{1,i}, \ldots, x_{15,i})$ (Eq.2.1).

Therefore, at each site one species outperforms all others. The number of sites where each species has the highest performance varies between species, since the environmental variables are not uniformly distributed. For some species, there is no site where they are the most competitive. Importantly, all individuals of a given species j respond in the same way to the environment, the performance of conspecifics differing only because they thrive in a different environment. Individual variation is thus fully environmentally-driven and structured in space (0% uIV and 100% sIV in Fig. 19C).

$$\begin{aligned} p_{ij} &= -(d_{ij} - \mu_d)/\sigma_d \\ d_{ij} &= \sqrt{(x_{1,j}^* - x_{1,i})^2 + \cdots + (x_{15,j}^* - x_{15,i})^2} \end{aligned} \tag{Eq.2.1}$$

where μ_d and σ_d are the mean and variance of $d_{i,j}$ across all sites i and species j respectively.

II.2.b. The *Imperfect knowledge models*

Just like a field ecologist is typically not able to fully characterize all dimensions of environmental variation, we then assumed that only $n_{obs} < 15$ environmental variables were monitored and accounted for when estimating individual performance. These performances are thus estimated from a statistical model fitting the individual performance provided by the *Perfect knowledge model* $p_{i,j}$ (Eq.2.1, representing what actually happens in the field and is measured, assuming no measurement error) against the n_{obs} observed environmental variables (Fig. 19). We consider the simple case where ecologists assume a quadratic relationship between performance and each observed environmental variable, thus approaching the triangular shape of the actual relationship of the *Perfect knowledge model* (Eq.2.2).

$$\begin{aligned} &p_{ij} = \beta_{0,j} + \beta_{1,j} x_{1,i} + \beta_{2,j} x_{1,i}^2 + \cdots + \beta_{2n_{obs}-1,j} x_{n_{obs},i} + \beta_{2n_{obs},j} x_{n_{obs},i}^2 + \varepsilon_{ij} \\ &\varepsilon_{ij} \sim \mathcal{N}(0, V) \end{aligned} \tag{Eq.2.2}$$

This statistical model was fitted using the lm function of the stats R package. Species parameters $\beta_j = [\beta_{0,j}, \ldots, \beta_{2n_{obs},j}]$ and residuals (ε_{ij}) were retrieved. In this model, we considered that the ε_{ij} represented an unstructured IV. The observed IV was thus estimated as the variance of the ε_{ij} for each species j, V_j. This variability emerges from the spatial variation in environmental variables that were not monitored and accounted for, namely $[x_{n_{obs}+1}, \ldots, x_{15}]$.

In order to answer our second question (Fig. 19C, arrows 2 and 3), we varied the level of knowledge of the environment, *i.e.* varied n_{obs} from 0 to 15. ε_{ij} thus accounted for the $15 - n_{obs}$ unobserved environmental variables, respectively. In the *Imperfect models without uIV*, the residual variation, ε_{ij}, was neglected (Eq.2.3), while in the *Imperfect knowledge models with uIV*, it was included as a random noise $\hat{\varepsilon_{ij}}$ estimated from independent individual draw in a normal distribution of variance V_j (Eq.2.4).

Therefore, in the *Imperfect knowledge models without uIV*, conspecific individuals respond similarly to the environment as in the *Perfect knowledge model* for the observed environmental dimensions, but lacking information on the other environmental dimensions (0% uIV in Fig. 19C). In contrast to the *Perfect knowledge model* and the *Imperfect knowledge models without uIV*, in the *Imperfect knowledge models with uIV*, conspecific individuals can perform differently in the same environment (0 to 100% uIV in Fig. 19C).

$$\hat{p_{ij}} = \beta_{0,j} + \beta_{1,j} x_{1,i} + \beta_{2,j} x_{1,i}^2 + \cdots + \beta_{2n_{obs}-1,j} x_{n_{obs},i} + \beta_{2n_{obs},j} x_{n_{obs},i}^2 \tag{Eq.2.3}$$

$$\hat{p_{ij}} = \beta_{0,j} + \beta_{1,j} x_{1,i} + \beta_{2,j} x_{1,i}^2 + \cdots + \beta_{2n_{obs}-1,j} x_{n_{obs},i} + \beta_{2n_{obs},j} x_{n_{obs},i}^2 + \hat{\varepsilon_{ij}} \tag{Eq.2.4}$$

The three types of performance models (Eq.2.1, Eq.2.3, Eq.2.4) were then implemented in a simulator of community dynamics, in order to disentangle the effects of random, unstructured IV and of the imperfect characterization of the environment on community dynamics and species coexistence.

II.3. Community dynamics simulation

Our simulator of community dynamics was inspired by Hurtt and Pacala (1995). However, several of our modeling choices differed. First, we explicitly used several environmental dimensions to account for niche multidimensionality, while they used a summary environmental index. Second, we randomly drew species optima, therefore leading to various sizes of the environmental space where each species outperforms all the others, while they used equally wide ecological niches across species. This allowed us to test several configurations of niche partitioning. Finally, mortality and recruitment were stochastic in their model, while we chose a deterministic process to stabilize coexistence and limit the sources of uncertainty to the effect of IV, although we also tested a stochastic alternative (see details below).

For a given simulation of community dynamics, the simulated community was initialized with ten individuals of each of the 20 species, located randomly in the landscape. The performance of these individuals was computed using either the *Perfect knowledge model* (Eq.2.1), an *Imperfect* *knowledge model without uIV* (Eq.2.3), or an *Imperfect knowledge model with uIV* (Eq.2.4). Mortality events result in vacant sites for which species then compete for recruitment. To test the robustness of our results to the choices made in building the community dynamics simulator, we implemented alternative ways to simulate mortality and fecundity. For mortality, we explored the three following approaches: (i) the one percent less performing individuals in the landscape die at each timestep, henceforth denoted *deterministic mortality*; (ii) one percent of the individuals die at each timestep, and the probability of each individual to die is proportional to its performance, henceforth denoted *stochastic mortality*; (iii) the probability θ_{ij} of each individual j to die is computed as a function of its performance, $\theta_{ij} = \text{logit}^{-1}(\text{logit}(0.01) - 0.5 \times p_{ij})$, henceforth denoted *logistic stochastic mortality*. Death events are then drawn in a binomial distribution $B(n_s, \theta)$ with θ the vector of all θ_{ij}. For fecundity, we explored the two following approaches: (i) the number of propagules $prop_{j,t}$ depends on species abundance $A_{j,t}$: $prop_{j,t} = round(0.5 \times A_{j,t})$, henceforth denoted the *abundance-dependent fecundity*; or (ii) each species present in the community produces ten offspring per timestep, henceforth denoted the *fixed fecundity*. In both cases, propagules are then randomly distributed among all vacant sites (*i.e.* there is no limited dispersal). If several propagules land on the same vacant site, the propagule with the highest individual performance outcompetes the others and wins the site. Hence a species that is not the best at a site can win "by forfeit". When individual performance is computed using the *Perfect knowledge model*, the colonization of a vacant site only depends on the species optima. When individual performance is computed using an *Imperfect knowledge model without uIV*, this colonization depends on the estimated species parameters (the β_j), and, for an *Imperfect knowledge model with uIV*, also on a random individual variation (the $\hat{\varepsilon_{ij}}$), that enables potential inversions of competition hierarchy locally.

Overall, multidimensional niche partitioning and environmental filtering are the main coexistence mechanisms within the simulated communities: mortality and recruitment are controlled by performance, which depends on the local environment in a species-specific way. Therefore, individuals that are maintained and recruited on a site are filtered by the environment, and performance on each site increases rapidly. When using the performance models without uIV (*i.e. Perfect knowledge* and *Imperfect knowledge models without uIV*), each species rapidly occupies a preferred habitat defined by its optima (perfectly or imperfectly estimated) in many environmental dimensions. It should be noted that species favorable habitats are not equally frequent across species, thus intrinsically defining rare and dominant species in the landscape. Few species that have a rare favorable habitat and whose initial individuals randomly land on unfavorable sites, can be excluded from the community.

As most results remained qualitatively unchanged across the different alternatives for simulating mortality and fecundity, we present below the results for the *deterministic mortality* and the *abundance-dependent fecundity* only, and refer the reader to Appendix 1 for the other alternatives.

II.4. Experimental setup and analyses

For each model of individual performance and number of observed environmental dimensions, we used ten different Environment × Species optima ($E \times S$) configurations, each prescribed randomly. Within each $E \times S$ configurations, ten simulations differing only in their initial conditions (location of the initial individuals) were run. Each simulation of community dynamics was run for 10,000 generations (Table 7). The ten $E \times S$ configurations were the same across models of individual performance and number of observed environmental dimensions and the ten initial conditions were the same across $E \times S$ configurations. In total, this leads to 3300 simulations.

Table 7: Experimental setup.

Experimental setting	Number	Comments
Model of individual performance	3	*Perfect knowledge*, *Imperfect knowledge without uIV*, *Imperfect knowledge with uIV*
Number of observed environmental dimensions $\boldsymbol{n_{obs}}$	0 to 15	Except for the *Perfect knowledge model*
$\boldsymbol{E} \times \boldsymbol{S}$ configuration	10	The same configurations are used across the models of individual performance and number of observed environmental dimensions
Initial conditions	10	Determined by the locations of the 10 individuals per species within the landscape
Generations	10000	Sufficiently long so that changes in the community are very slow

In order to compare simulation outputs, we studied several aspects of final communities: (1) community diversity, (2) the similarity in community composition between simulations, and (3) site sorting. Community diversity was estimated using species richness and the Hill-Shannon diversity index (Roswell et al. 2021). Similarity in community composition was estimated as the pairwise percentage similarity of final species abundances between pairs of simulations. For two vectors of species abundances $A = (a_1, \ldots, a_i, \ldots, a_S)$ and $B = (b_1, \ldots, b_i, \ldots, b_S)$, the percentage similarity was computed as

$$PS = \frac{2 \times \sum_{i=1}^{S} min(a_i, b_i)}{\sum a_i + \sum b_i} \qquad \text{(Eq.2.5)}$$

To quantify site sorting, we computed for each simulation the final community mean performance as the performance obtained with the *Perfect knowledge model*, averaged across all individuals at the end of the simulation. This community mean performance thus corresponds to the strength of the environmental filtering in community assembly, *i.e.* the site sorting: the higher the mean performance, the stronger the effect of the environment on community assembly.

III. Results

III.1. Final community diversity

Final community diversity, both in terms of species richness and Hill-Shannon index, was lower with unstructured IV than with the *Perfect knowledge model* whatever the number of observed environmental dimensions *i.e.* relative importance of structured and unstructured IV (Fig. 21A and B). This diversity increased with the number of observed dimensions. In most cases, adding unstructured IV reduced the species diversity with respect to the corresponding *Imperfect knowledge model without uIV* (Fig. 21C and D). However, this effect varied with the number of observed dimensions (but see in case of alternative mortality implementation, Appendix 1): below 50% of explained variance (*i.e.* up to three observed environmental dimensions, Fig. 20), adding unstructured IV resulted in a higher or similar diversity than with the *Imperfect knowledge models without uIV*. This difference first decreased and then increased as the number of observed dimensions increased, while staying negative from 3 to 15 observed dimensions.

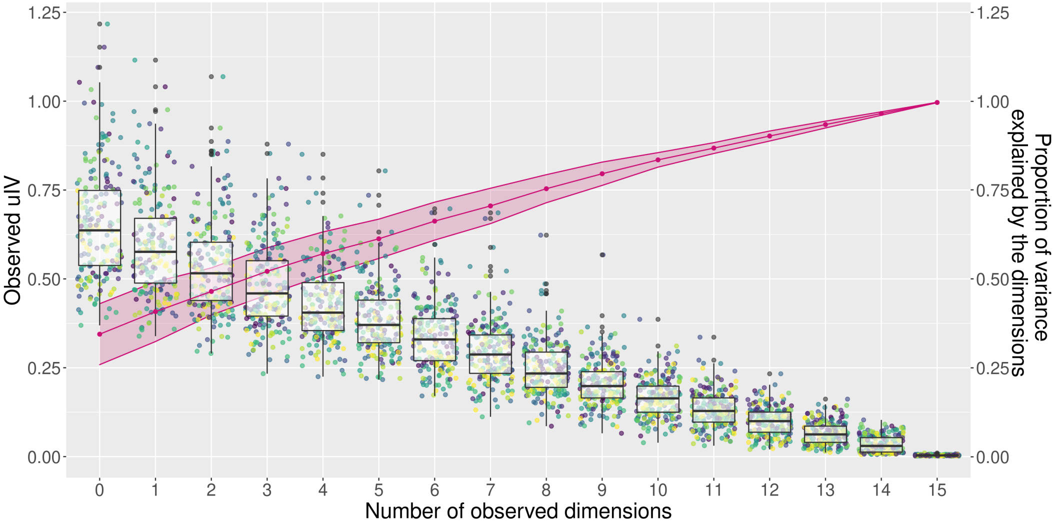

Figure 20: Observed IV depending on the level of knowledge of the environment. Each point represents the unstructured IV inferred for one species, and each color represents an configuration (twenty points per color for the twenty species). Unstructured IV was inferred using a statistical model (Eq.2.2) taking 0 to 15, out of 15, dimensions into account to fit the performance provided by the *Perfect knowledge model*; the pink points, curve and ribbon correspond to the mean and standard deviation of the R2 of these statistical models (computed over the ten different configurations for each number of observed dimensions). As expected, observed unstructured IV decreases with the number of observed dimensions, *i.e.* with the level of knowledge of the environment.

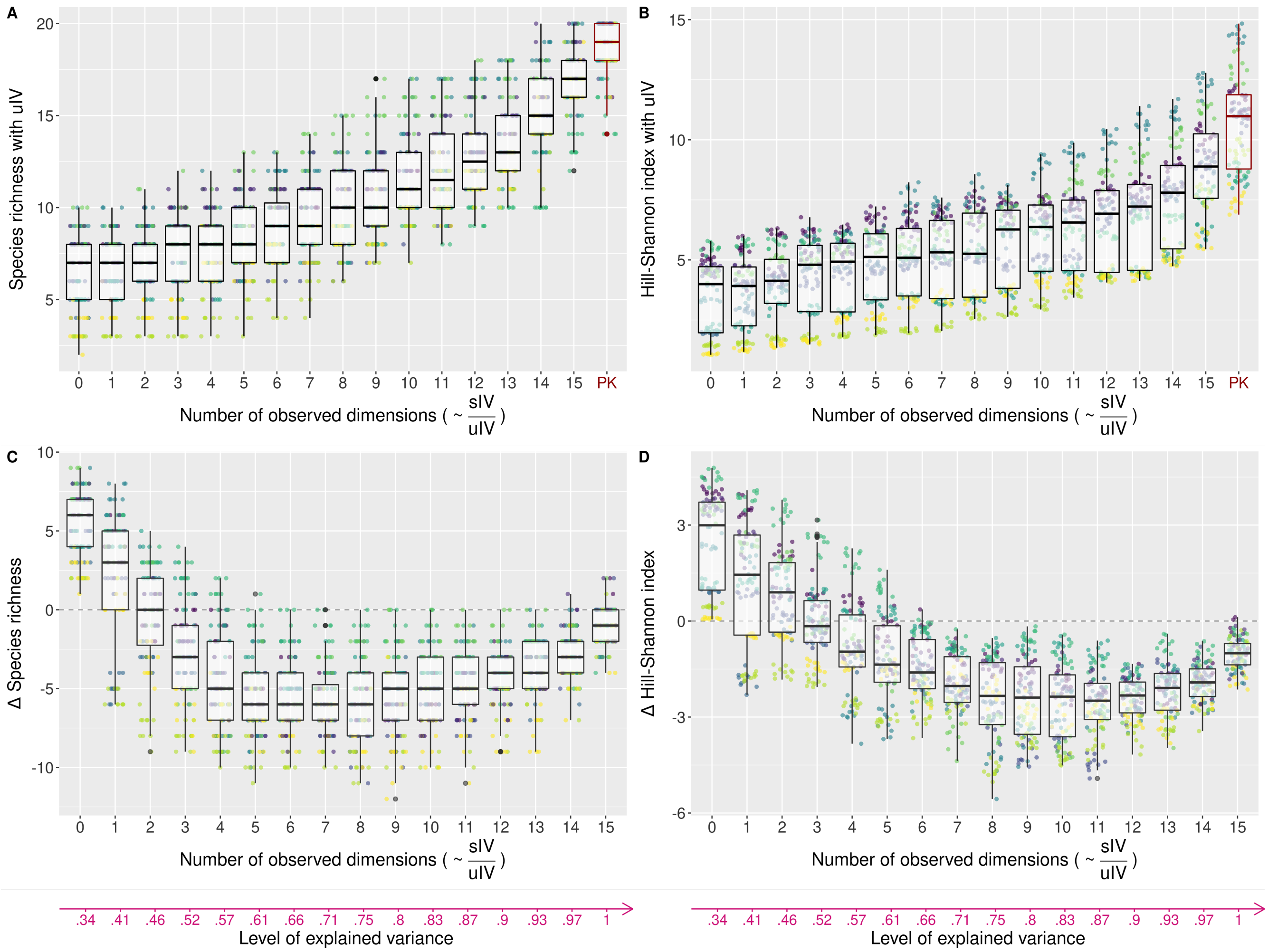

Figure 21: Effect of the structure of individual variation on community diversity. Each point represents the diversity, either computed as the species richness – left panels – or the Hill-Shannon diversity index – right panels – of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 20) depicted with the pink arrow at the bottom. The top panels show the final community diversity obtained with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). This is useful to examine our first question (Fig. 19C, arrow 1). The bottom panels show the difference in the final community diversity obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher diversity when adding unstructured IV. This is useful to examine our second question (Fig. 19C, arrows 2 and 3), by comparing the effect of adding unstructured IV at different levels of knowledge of the environment. The *Imperfect knowledge models with uIV* never reach the diversity obtained with the *Perfect knowledge model* (A and B). Moreover, adding unstructured IV as a random noise has an effect on community diversity that varies with the number of observed environmental dimensions (C and D). Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity* (see main text).

III.2. Final community composition

Similarity (as measured by PS, Eq.2.5) of the *Imperfect knowledge models with uIV* with the *Perfect knowledge model* was low when few environmental dimensions were observed, *i.e.* the relative importance of structured *vs.* unstructured IV was low. This similarity increased with the number of observed dimensions (from 0.55 to 0.9, Fig. 22A). Adding unstructured IV increased the similarity with the *Perfect knowledge model* at low numbers of observed dimensions (from 0 to 2 dimensions, *i.e.* below 50% explained variance) but decreased it at higher numbers of observed dimensions, with respect to the corresponding *Imperfect knowledge model without uIV* (Fig. 22C, but see in case of alternative mortality implementation, Appendix 1). This negative effect became stronger (from 3 to 8 observed dimensions) before becoming weaker (from 9 to 15 observed dimensions). See Appendix 2 for the similarity within models.

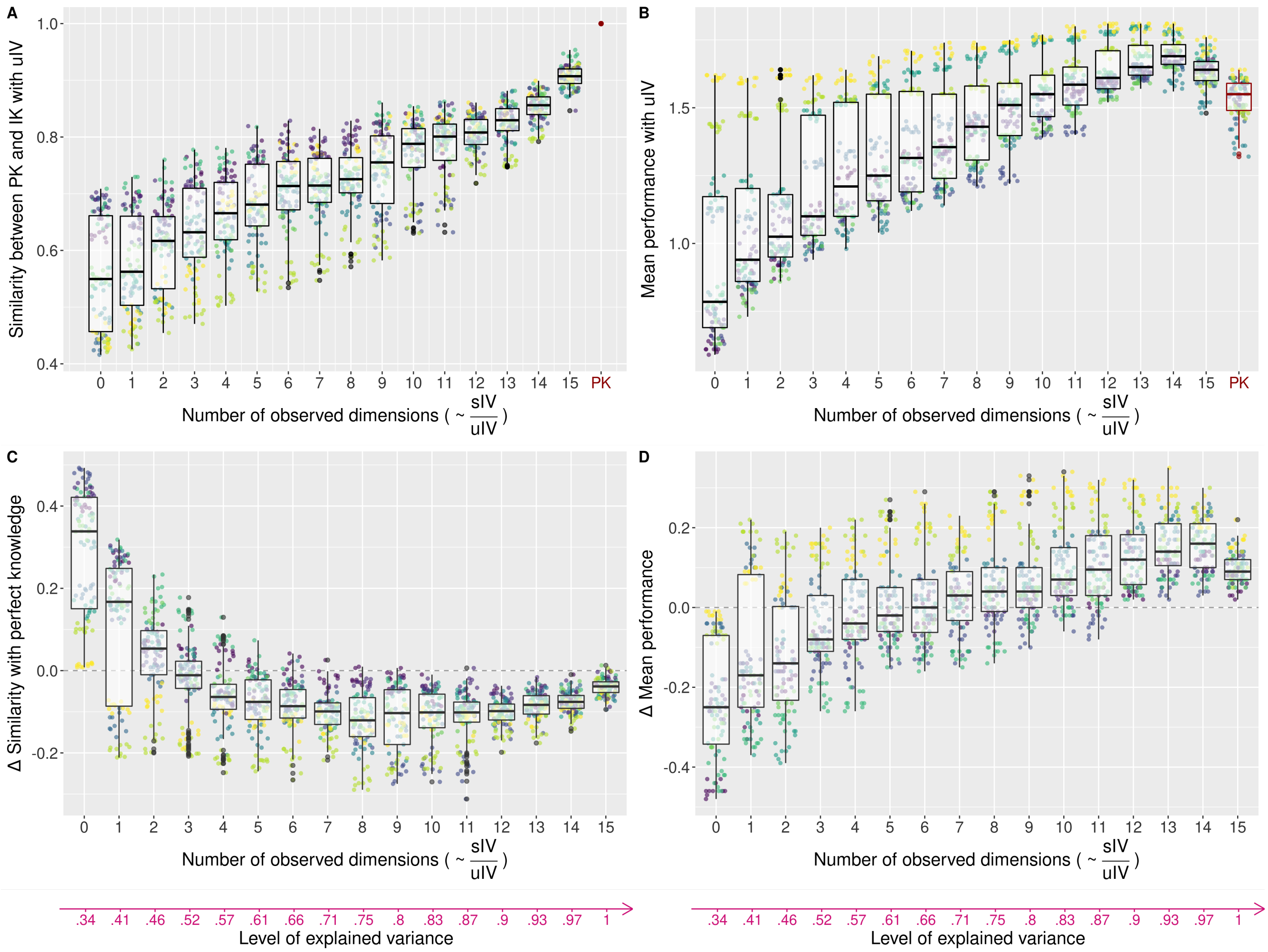

Figure 22: Effect of individual variation on the similarity in final species abundances between models and on the site sorting. Each color represents an $E \times S$ configuration. For the similarity - left panels -, each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. The top panels show these two metrics for communities simulated with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in these metrics for communities obtained with the *Imperfect knowledge models with* and *without unstructured IV*. Points that are above zero (horizontal dashed line) correspond to a higher similarity or mean performance when adding unstructured IV, respectively.The similarity between the *Perfect knowledge model* and the *Imperfect knowledge models with uIV* is low with few observed dimensions and increases with the number of observed dimensions (A). The effect of adding unstructured IV to *Imperfect knowledge models* on the similarity with the *Perfect knowledge model* varies with the number of observed environmental dimensions (C). The mean performance obtained for communities simulated with the *Imperfect knowledge models with uIV* as well as its difference with the *Imperfect knowledge models without uIV* vary with the number of observed dimensions (B, D). Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity* (see main text).

The mean performance of communities simulated with the *Imperfect knowledge models with uIV* increased with the number of observed dimensions (except between 14 and 15 observed dimensions), *i.e.* the relative importance of structured and unstructured IV (Fig. 22B). Below ten observed dimensions, it remained lower than that of the communities simulated with the *Perfect knowledge model*, but was higher above ten observed dimensions. Adding unstructured IV decreased the mean performance of the final species community from zero to six observed dimensions but increased it at higher numbers of observed dimensions, with respect to the corresponding *Imperfect knowledge model without uIV* (Fig. 22D). This difference increased with the number of observed dimensions, except between 14 and 15 observed dimensions.

IV. Discussion

IV.1. Substituting structured with random unstructured individual variability lowers community diversity and generates unrealistic communities

Ecologists have only access to an imperfect characterization of all the dimensions that actually lead to individual variation. This lack of knowledge results in an observed but unexplained intraspecific variability. To cope with it, it has often been (implicitly) assumed that some unstructured variation could be added to the explained part of variation to reach the actual observed total variation. To test this assumption, in our simulation experiment, we varied the level of knowledge of the environment and incorporated the remaining (unaccounted) variability in individual performance as unstructured noise, thus varying the ratio of structured and unstructured IV. We showed that this difference in the nature of IV has strong consequences on community structure and composition.

Compared to the communities simulated with a 15-dimensional individual performance (*Perfect knowledge model*), the communities simulated with a performance estimated with fewer dimensions and to which the remaining variance was added as a random noise (*Imperfect knowledge models with uIV*) were less diverse (Fig. 21A and B; see also Appendix 3 for further explanation on simulated species richness). Beyond the community diversity *per se*, community composition was unrealistic when the number of observed dimensions was low, *i.e.* when the relative importance of structured *vs.* unstructured IV was low: the strength of environmental filtering in shaping community assembly was too low to generate species abundances similar to the one of the *Perfect knowledge model*. As the relative importance of structured IV increased, both the strength of environmental filtering and the similarity of the final species abundances with the ones obtained with the *Perfect knowledge model* increased (Fig. 22A and B).

Finally, random intraspecific variability is not a good substitute for species response to unobserved environmental dimensions for studying community dynamics. Moreover, interpreting observed IV as unstructured differences in conspecifics' response to the environment can lead to misinterpretations regarding the ecological mechanisms driving the community dynamics: it would mistake the response of species to environmental variation (a niche mechanism) with random variability (a neutral mechanism), and present IV as a coexistence mechanism *per se* independently of the differences in species response it can actually result from. Hence, maintaining the variance observed among individuals is not sufficient to capture the community dynamics, the structure and nature of this individual variability is also critical.

IV.2. The effect of adding a random IV depends on the relative importance of structured *vs.* unstructured individual variability

Previous studies that typically explored the role of IV on community dynamics actually did not even maintain the total level of variance among individuals. Such studies typically compared communities with and without additional random variability, for a same level of explained individual variation (*Imperfect knowledge model without uIV vs. Imperfect knowledge model with uIV*). Our results showed that the effect of adding a random IV depends on the level of explained variance, *i.e.* in our case on the number of observed dimensions (Fig. 21C and D, Fig. 22C and D).

When structured IV accounted for less than 50% of the total individual variation, the addition of a random unstructured variation increased community diversity (Fig. 21, but see in case of alternative mortality implementation, Appendix 1). This positive effect was due to the inversions in competitive hierarchy produced by adding a random variation to individual performance; it allowed more species to be maintained in the community although there were few theoretical winners (*i.e.* species that are the best performing somewhere in the landscape) because of the projection of their niches on few environmental dimensions. Similarly to species diversity, when the proportion of structured IV was low, adding unstructured IV increased the similarity of the final species abundances between the *Imperfect knowledge model* and the *Perfect knowledge model* (Fig. 22C). This increase in similarity was however only due to the higher number of species reached when adding unstructured IV (Fig. 21) (the higher number of zero abundances with the *Imperfect knowledge models without uIV* decreases the estimated similarity with the abundances obtained with the *Perfect knowledge model*).

When the proportion of structured IV increased, this positive effect of adding random IV on community diversity vanished (Fig. 21, but see in case of alternative mortality implementation, Appendix 1), because the destabilization of the niche partitioning between species due to unstructured IV decreased. Indeed, as expected, the lower unstructured IV was, the greater community mean performance (*i.e.* site sorting) was in comparison to the communities simulated without unstructured IV (see Appendix 3 for further explanation on the absolute differences in community mean performance). This negative effect first increased but then decreased with the number of observed environmental dimensions, because the magnitude of the added unstructured IV became lower (Fig. 20).

Finally, adding unstructured IV in models is most likely to move simulated community composition away from reality (here represented by the *Perfect knowledge model*), because this type of variation blurs the species properties that are (although imperfectly) captured with the observed dimensions. In other words, adding randomness never compensates for lack of knowledge and can even blur the limited knowledge obtained from field data, although this is not the case at a very low level of knowledge of the environment.

Previous studies testing the effect of adding intraspecific variability on species coexistence provided contrasting results (Lichstein et al. 2007; Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019). Stump et al. (2022) proposed a framework to explain part of these discrepancies, by differentiating the nature of the traits - niche *vs.* hierarchical traits – on which variation was added. While our virtual experiment only considered additional variability in a hierarchical trait (performance) *sensu* Stump et al. (2022), our results here evidenced an additional source of discrepancies when testing the effect of adding a random variability on community dynamics: the relative importance of explained and structured *vs.* unexplained and unstructured individual variance. Future studies should thus pay great attention to the nature and structure of the observed variability when testing its effect on communities and move away from the systematic approach of adding an unstructured noise.

IV.3. Accounting for a high-dimensional environment in community dynamics models

Most previous studies have modeled IV as a random noise around species means (Lichstein et al. 2007; Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019), and did not represent environmental variations that generate individual variation (*e.g.* Lichstein et al. 2007; Courbaud et al. 2012), or did so in a way that does not mirror multidimensional variation: Uriarte and Menge (2018) provided two different habitats, Vieilledent et al. (2010) used site effects at a much larger scale than individuals, Crawford et al. (2019) represented biotic interactions with resources that are constant through space and time, and while Banitz (2019) is the first to test the consequences of IV resulting from a spatially-structured environmental index, coexistence relied on trade-offs and random disturbances in a one-dimensional environment. Our results showed that, when the level of knowledge of the environment that generates individual variation is high enough (Fig. 21C, D and Fig. 22C), adding unstructured IV, instead of improving the realism of the simulated communities, can actually move them away from the actual communities (*i.e.* the ones simulated with the *Perfect knowledge model* of individual performance). Thus using independent random draws is not a relevant approach to represent intraspecific variability that is often environmentally-driven (Girard-Tercieux et al. 2023), and progress must be made to take into account the environment-species interactions in models.

IV.3.a. Improving the knowledge of the environment: a costly but worthy endeavor

The environment can vary in many ways, even if the number of resources is limited, as it is likely the case (Craine 2009). Indeed, many other biotic and abiotic variables can influence individual performance (soil microbiome and texture, micro-climate, pathogens, Fortunel et al. 2018; Averill et al. 2022). Moreover, species can partition the same environmental dimension (*e.g.* light) by responding non-linearly to it (*e.g.* with different light-performance slopes at different light levels), further increasing the dimensionality of their responses to environmental variation in space and time. As monitoring environmental variables and species responses at fine spatio-temporal scales is difficult and costly, most of the environmental variation that actually influences individuals' attributes is not properly monitored in ecological studies.

Our results suggest that improving the characterization of environmental variation by monitoring additional independent environmental variables (*i.e.* to moving to the right in Fig. 20, 21, and 22) is a worthy endeavor. Using one dimension out of 15, 41% of the variation in individual performance is accounted for. The corresponding simulated communities, in absence of any additional random variation, reached less than half the species richness of the communities simulated with the actual 15-dimensional individual performance (median of 4 *vs.* 18, Fig. S4.1) with relatively dissimilar community composition (median of similarity in abundance of 0.43 *vs.* 0.95, median of mean performance of 1.15 *vs.* 1.54, Fig. S4.2). Adding a second dimension allowed to increase the proportion of explained variance in individual performance to 46%, and simulated species richness to a median of 7, with more realistic communities (median of similarity in abundances of 0.59 and median of mean performance of 1.19). The identification of the most influential environmental variables or dimensions in species responses using ecological knowledge (Rüger et al. 2009; Bartlett et al. 2016; Soong et al. 2020) is of course valuable to optimize and prioritize these efforts in the field.

Another way to improve the characterization of the environment could be to better capture the spatio-temporal structure of the already monitored variables, *i.e.* to monitor them at finer scales in space and time. In our simulation, the scale of the environmental variation was the same as the individual (prescribed by the grid mesh size) across all models of individual performance. Testing the effect of degrading the resolution of the observed environmental variation in the case of an imperfect characterization of the environment could be explored in the future. Finally, improving the characterization of species responses to a few major environmental variables can also enable to better reveal the realized niche partitioning operating within communities. While niche partitioning is more easily achieved with a high number of environmental dimensions, high level of coexistence can also be reached with only one axis if it is well partitioned among species (*e.g.* Hurtt and Pacala 1995; Detto et al. 2022), thus building a high-dimensional space where each species can perform better somewhere. This is in agreement with several studies that showed significant improvement in the realism of simulated communities by only adding a second dimension to species responses in community models (Falster et al. 2017; Rüger et al. 2020).

While efforts to improve our characterization of environmental variation and species responses are, and need to be, continuously pursued (Tymen et al. 2017; Estes et al. 2018; Zellweger et al. 2019), making a better use of the ecological information contained in existing datasets should also be attempted in parallel.

IV.3.b. Structuring variation: a first step towards accurate representation of multidimensionality

Our virtual experiment corresponds to an extreme case in which conspecific individuals have exactly the same response to environmental variation, which is unlikely to be the case under the joint effect of environmental and genetic variation in the field. However, while the intraspecific variation that is added as a noise around species means is not structured in space and time, IV, whether it is environmentally- or genetically-driven or both, is actually highly likely to be structured in space and time (Girard-Tercieux et al. 2023). This structure could appear when IV results from spatially-structured environmental variables or from limited dispersion or local adaptation (Marrot et al. 2021; Schmitt et al. 2021; Westerband et al. 2021). As shown here, this has profound consequences on the properties of the simulated community. Importantly, the spatio-temporal structure of individual variation is an emergent property of conspecific individuals responding more similarly to the environment than heterospecifics (Clark 2010; Girard-Tercieux et al. 2023), an important condition for stable species coexistence (Chesson 2000b).

Observed or inferred IV, whatever its source (genetic, environmental or an interaction of both, Westerband et al. 2021), can be structured at the individual scale (”individual variability”) using individual effects when one individual is repeatedly observed at one site. While such individual effects are then typically randomly attributed to individuals in the landscape (*e.g.* Clark et al. 2003), which is almost equivalent to adding a random noise, the structure in these inferred individual effects can be conserved when injected in a community dynamics model. In doing so, a part of observed IV is spatially structured. Pioneer studies have started using this approach to structure IV (Purves and Vanderwel 2014; Uriarte and Menge 2018; Banitz 2019), and future work should further explore this direction to generalize its use in community dynamics models. Another source of environmental variation that was not tackled in this study is temporal variation. This variation is often structured, at different temporal scales (seasons, years, El Niño/La Niña events, *etc.*) and this structure should be accounted for in models by expliciting those temporal scales after detection in the data.

Finally, the fact that all species respond to the same environmental variation, and that conspecifics tend to respond more similarly to it, can influence the structure of the covariance matrix of species abundances (Clark 2010). Exploring the structure of this covariance matrix could therefore be a way to improve community dynamics models while waiting for new environmental data and species knowledge.

Overall, our results suggest that it is crucial to explore the structure of observed IV in real communities to better understand its impact on diversity and community dynamics.

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Supplementary information and code access

Appendix 1: Alternative implementations of mortality and fecundity
Appendix 2: Stability of the simulations
Appendix 3: Role of suboptimal species depending on the implementation of mortality and fecundity
Appendix 4: Comparisons between communities simulated with the *Imperfect knowledge models without uIV* and with the *Perfect knowledge model*

The code used for this study is available in a GitHub repository (`https://github.com/camillegirardtercieux/coexist`) and has been permanently archived on Zenodo (`https://doi.org/10.5281/zenodo.6929042`).

Declaration of interests

All authors declare that they have no conflict of interest.

Chapter 3

A universal coexistence hypothesis resolves the biodiversity paradox: Species differences that generate diverse forests

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Contribution to the chapter

Discussions within the INTRACO working group following the framework I developed in Chapter 2 led to the initial ideas of this study. James S. Clark then developed the model and analyzed its outputs, with substantial contribution from the group. James S. Clark wrote a first draft of the manuscript. All coauthors contributed to discussion of ideas and revisions of the manuscript.

This chapter is in preparation.

Chapter outline

As illustrated in Chapter 1, intraspecific variability can be structured in space and time due to variations of the environment in many dimensions. This structure impacts the outcomes of a community dynamics model in Chapter 2, motivating the recommandation to take this structure into account in models. In this third and last chapter, we explore in a simulation framework how variations of the environment in many dimensions combined with species differences structure intraspecific variability and impact species coexistence. We also test if including this emerging structure of intraspecific variability using a covariance matrix only is sufficient to maintain species coexistence and reproduce other properties in a model.

Abstract

Ecological theory aims to understand how and why species differences allow competitors to coexist, but explanations remain inconsistent with data. Tightly constrained parameter tradeoffs needed for coexistence in models contrast with evidence that forests can support high diversity and be invaded repeatedly by species that lack specialized tradeoffs. By translating environmental responses to individual covariance, a universal coexistence hypothesis shows i) that species differences lead to a natural tendency to concentrate competition within the species, the common feature needed to promote coexistence in models, and ii) the fingerprint of this effect is available in covariances between individuals that can be observed in nature. The many ways in which species differ make high diversity almost inevitable. This covariance not only provides the evidence for this mechanism; it further provides a new direction for earth surface models that currently cannot sustain diverse communities despite large numbers of evidence-based parameters.

Keywords — competition, demography, forest diversity, species coexistence.

I. Introduction

Ecology lacks theory that predicts high species diversity from data as an inevitable consequence of the variation that is ubiquitous in nature (Fig. 23). The need to understand diverse forests when ecological models can explain only limited coexistence (Tilman 1985; Falster et al. 2017) has become more than an academic exercise. The earth system models used to anticipate future forest function suffer the same problem, despite dozens to hundreds of parameters that are, to the extent possible, extracted from empirical data or evidence-based theory (Fisher et al. 2018). A universal coexistence hypothesis developed here translates the high-dimensional variation that is well-known to ecologists and systematists into its observable effects that generate the diversity needed to study forest change.

A challenge shared by simple, theoretical models of competition (May 2001; Tilman 1985; Serván et al. 2018), large stand simulators (Maréchaux and Chave 2017; Rüger et al. 2020; Courbaud et al. 2022), and dynamic earth system models used to predict global change (Fisher et al. 2018; Longo et al. 2019; Fisher and Koven 2020; Rollinson et al. 2021) is the problem of predicting the high diversity observed in nature. Ecologists have long recognized that plant populations can be limited by a small number of resources (Tilman 1985; Nogueira et al. 2018), seemingly utilized in similar ways by many competing species. In closed forests, trees compete for light, in part, through height growth. They procure water and nutrients through expanded root systems. Tree growth and fecundity respond to variation in one to a few resources, but not to dozens of resources (Bloom et al. 1985; Tilman et al. 1998; Qiu et al. 2022). Despite intense density-dependent mortality from competition for apparently few limiting resources (Assmann 1970; Westoby 1984; D'Amato et al. 2013; He et al. 2022), diversity can be high, and stands are still frequently invaded by introduced species. Yet the many structural and physiological differences that are parameterized in large models do not lead to coexistence. Instead, maintaining diversity in the absence of parameter values carefully selected for this purpose depends on the assumption that seeds remain available even when the adults that would produce those seeds are not (Pacala et al. 1996; Maréchaux and Chave 2017; Longo et al. 2019; Rüger et al. 2020).

Models that achieve coexistence of competitors for few resources do so in one of two related ways. The first way is through a narrow specification of parameter values, usually in the form of tradeoffs, to assure that each species wins somewhere. For plant species competing for only two resources, coexistence in the resource-ratio model (Tilman 1985) requires a strict trade-off in minimum resource requirements for each species. Despite this restrictive tradeoff assumption, coexistence still only occurs if the environment offers the precise supply rates that would make a different species pair stable at each ratio of resource requirements. Higher diversity requires more specifically aligned tradeoffs to allow that every species has the advantage somewhere (MacArthur 1969; Falster et al. 2017; Detto et al. 2022). Coexistence in models is also achieved with narrowly specified competitive intransitivities to insure that there are enough competitive reversals between species such that each species can win for some combination of interactions (Laird and Schamp 2006; Bunin 2017; Serván et al. 2018; Gavina et al. 2018; Laan and de Polavieja 2018; Amarasekare 2002).

A second, albeit related (see below), way to predict diversity in models is to build in the assumption that competition is weak. Diverse communities are predicted by the Lotka-Volterra model if there is diagonal dominance in the species-by-species interaction matrix (Serván et al. 2018; Clark et al. 2020): so long as the diagonal of the interaction matrix is sufficiently negative, there is strong intra-specific competition, and each species limits itself. Diagonal dominance can arise in consumer-resource models when there are more limiting resources than there are species competing for them (MacArthur 1969; Advani et al. 2018). This self-regulation can operate in models indirectly, as when a species' suffers disproportionately whenever it increases in abundance (Gavina et al. 2018). Relatedly, models can assume that every species is the competitive dominant somewhere on the landscape without addressing the question of how this occurs. Examples include assigning species dominance rankings or the settings in which there is dominance by every species in ways to assure that each wins somewhere (Hurtt and Pacala 1995; Sears and Chesson 2007; Mouquet et al. 2002; Fukami and Nakajima 2011). The two ways to obtain coexistence, through narrow parameter constraints or weak competition, are related in this sense: where restrictive parameter values are required for coexistence, they do so by limiting competition between species.

Models that generate diversity, either by narrowly defined parameter tradeoffs or by assuming that inter-specific competition is too weak to limit diversity, do not address the diversity paradox in forests. On the one hand, if forest diversity depended on narrowly defined tradeoffs, then those precisely aligned tradeoffs should be evident in data, and species invasion would rarely occur. Recent evidence for structure in multivariate trait analyses show a number of weak correlations (Wright et al. 2007), but none approaching the strict tradeoffs that would be needed to achieve coexistence in models (Clark 2010; Clark et al. 2018). If coexistence depended on strict tradeoffs, then invading species would be limited to those possessing the specific parameter combinations needed to slot in between species already there. However, species invasions are common in forests, and the most diverse communities can be among the most highly invaded (Stohlgren et al. 1999; Lowry et al. 2013). The alternative to parameter tradeoffs, building in as many ways to persist as there are species (*e.g.*, by randomly assigning each species a place to dominate), sidesteps the problem of intense competition for few resources. Even so, proposed remedies in models often admit small diversity increases, not thousands of species, as in hyper-diverse Indonesian and New World Tropical forests. Further limitations include model parameters that cannot be estimated from data (*e.g.*, competitive intransitivities) or that admit only abstract interpretation (*e.g.*, Lotka-Volterra). Models constructed in either of these ways cannot guide further development of the earth system models used to understand climate change, which must build in responses to the key environmental variables that can be measured and tied to plant performance (Fisher et al. 2018; Longo et al. 2019).

At the same time that species compete intensely for a few resources, they also differ in thousands of ways. A single example, leaf shape, highlights species differences that can only evolve if they affect fitness and, thus, demographic rates (Fig. 23). Leaf size and shape affect carbon capture and water loss across the range of temperatures, light, and humidity levels that vary within and between habitats. The diversity of responses across these dimensions engage photosynthetic and transpiration rates, water loss, evaporative cooling, and risk of heat and frost damage. The complexity of sizes and shapes encountered within a single inventory plot (Fig. 23) are best explained as adaptive responses to the environment (Peppe et al. 2011). Ecologists do not need to assume that all variation like that in Fig. 23 is adaptive in order to recognize that much of it can be. The many species differences result in individual responses that are most similar to others of the same species. For example, most species suffer from late frost, but a given frost event may affect only the individuals of those species flowering on that date (Augspurger 2013; Bigler and Bugmann 2018). Many species benefit from long growing seasons, yet the growth benefits in a given year vary across species depending on differences in phenology and the day-to-day variation in moisture demand (Way 2011; Clark et al. 2014; Fu et al. 2018; Montgomery et al. 2020). And while drought affects most species, drought-induced mortality is often concentrated in one or a few species on a given site and drought event (Schwantes et al. 2017; Choat et al. 2018). The striking variation between species may not have tractable effects on their abundances within a community, because the many effects are cumulative, happening at the same times, and combining in complex ways, and they are sampled at much finer scales (typically, small plots) than the scale at which natural selection operates. Because the many species differences recognized by systematists and physiologists can only arise through adaptive evolution if they affect fitness, they have to affect demographic rates. Yet data reveal only vague trait correlations between a relatively small number of trait axes (Wright et al. 2007; Berdanier and Clark 2016), and not the strict parameter tradeoffs that are required for coexistence in models (*e.g.*, Tilman 2011; Clark et al. 2018; Falster et al. 2017). If models with intense competition for few resources predict that coexistence is hard in the absence of tight tradeoffs that are not evident in data, while nature shows both that high diversity is common and that diverse communities are often invaded (Stohlgren et al. 1999; Simberloff 2009; Lowry et al. 2013), then models miss a fundamental mechanism.

We offer an alternative explanation for coexistence that is universal, in the sense that it emerges from a ubiquitous property of communities: individuals tend to respond to environmental variation most like others of the same species (Clark 2010). In forests, where mortality increases in step with growth, this tendency can concentrate competition within the species, the common feature needed to promote coexistence in models. Two attractive features of this universal coexistence hypothesis include A) the potential to explain high diversity, not by narrow specification of species tradeoffs, but rather through the ubiquitous tendency for individuals to respond more like others of the same species, and B) the fingerprint of this mechanism is observable, in the covariances between individual trees. Importantly, this covariance relationship could hold even where individuals of all species tend toward positive correlation, as expected if responses include some widely-shared resources. The tendency for intra- to dominate inter-specific correlation between individuals emerges for both fecundity and growth across networks of forest stands in the southeastern US (Clark 2010), but the connection between observation and theory has not been demonstrated quantitatively. Here we demonstrate the quantitative link from A to B. This long-standing missing connection between observation and theory provides a way forward for models that exploit both the observable differences between species and the individual correlation needed to maintain species diversity.

II. A simple demonstration

Universal coexistence can be demonstrated using a model with as few as three elements: i) species responses that covary between individuals of the same and different species, ii) local competition that drives mortality, regardless of species identity, and iii) dispersal (Fig. 23B, Appendix). Individuals compete within a landscape where the environment varies over sites $k = 1, \dots, K$. The environment determines individual capacity to reproduce. Reproduction increases abundance locally and contributes to dispersal. Mortality increases with local crowding, but without underlying assumptions that a species mortality rate increases simply because that species is abundant–individuals of all species suffer equally from crowding. This competition that results from local population growth and the crowding that transfers to accelerated mortality is a ubiquitous feature of forests. The connection is so tight in even-aged stands that the proportionate mortality rate is precisely equal to the proportionate rate of increase in individual crown area (Clark 1990). In uneven-aged stands, the relationship between growth and mortality can vary widely. But it is still constrained by the fact that growth must translate to mortality, because biomass does not accumulate indefinitely. The growth-mortality relationship is embodied in forest yield tables that predict how mortality rate increases along with site fertility, through its effects on growth, and it informs selective thinning practice (Assmann 1970). Based on these three elements, the only way to promote diversity in the model is through the tendency for individuals that respond similarly to the environment to compete most intensely.

The multitude of structures and functions that differentiate species (*e.g.*, Fig. 23) can affect responses to the environment. Consider E ways for S species to differ across the K locations. E is the number of environmental predictors that might affect individual response, but only a small subset of these effects could be observed and measured. E is not the number of resources, but rather the number of dimensions the environment offers for responses to differ (Chesson 2000b; Letten and Stouffer 2019). E can be large, including climate variables and resources such as moisture, light, and nutrients. A given environmental variable can affect responses in multiple ways, such as climate norms (averages for a location), seasonality, and extremes. It can include non-linearities and interactions between variables. Landscape variation in these effects is held in a $K \times E$ matrix $\mathbf{E}$. Species responses to these variables are held in a $E \times S$ matrix $\mathbf{S}$. We exploit the transparency of mean responses and covariance matrices available from Gaussian distribution theory, as used for demographic estimates (Aakala et al. 2013; Sonti et al. 2019; Qiu et al. 2022), ecological theory, such as generalized Lotka-Volterra (Clark et al. 2020), and covariances among individuals (Clark 2010).

We demonstrate coexistence and why it occurs by comparing three ways of organizing individual variation. A joint distribution of S species responses at a site k can be summarized by a multivariate distribution,

$$\mathbf{h}_k \sim MVN_S(\mathbf{b} + \mathbf{S}'\mathbf{E}_k, \tau^2 \mathbf{I}_S) \tag{SK}$$

where vector $\mathbf{h}_k$ holds the S responses, one for each species, centered on mean responses $\mathbf{b} = \mathbf{1}_S b$. For simplicity, all species have the same value $b_s = b$. To simplify comparison with models that follow, and without loss of generality, we assume that the variables in $\mathbf{E}$ are centered on zero, a common centering used when models are fitted to data. We refer to this as the structured-known (SK) model, because it requires full knowledge of environmental effects on all species. $\mathbf{E}_k$ is the k^{th} row of matrix $\mathbf{E}$, τ^2 is residual (non-environmental) variation, and $\mathbf{I}_S$ is the identity matrix. Of course, species responses in eq. SK depend on their mean differences in the vector $\mathbf{S}'\mathbf{E}_k$. They are otherwise independent, because covariance matrix $\tau^2\mathbf{I}_S$ has zeros everywhere except along the diagonal. Eq. SK is written as a multivariate distribution to highlight the connection between known sources of variation in $\mathbf{E}$ and the case that follows, where causes and effects are unknown.

The knowledge of all E dimensions at each of K locations that affect each of S species is never available. However, environmental effects that cannot be accommodated in the mean of eq. SK, *i.e.*, those that cannot be observed and measured, contribute variation through the covariance,

$$\begin{aligned} \mathbf{h}_k &\sim MVN_S(\mathbf{b}, \mathbf{C}) \\ \mathbf{C} &= \mathbf{S}'\mathbf{V}_\mathbf{E}\mathbf{S} + \tau^2 \mathbf{I}_S \end{aligned} \tag{SU}$$

This structured-unknown (SU) model includes $\mathbf{V}_\mathbf{E} = cov(\mathbf{E})$, the covariance in unobserved environmental variables. Its effect on the first term of the species covariance matrix $\mathbf{C}$ combines environmental complexity with species responses and translates them into species covariance. For example, two species that respond similarly (similar columns in response matrix $\mathbf{S}$) to variables with meaningful variation across the landscape (large diagonal elements in $\mathbf{V}_\mathbf{E}$) have positive covariance in $\mathbf{C}$. Although one version of the model expresses species differences as mean values (SK) and the other as a covariance matrix (SU), eqs. SK and SU make the same assumptions about the relationship between species. The only difference between them is knowledge about the underlying basis for those relationships. We return to this mean-covariance connection after introducing individuals into the model.

The most direct translation from species in eqs. SK and SU to individuals comes from expanding the mean and covariance. If there are n_{sk} individuals of species s at location k, then there are $n_k = \sum_s n_{sk}$ individuals at k. The matrix of individual means is obtained by repeating n_{sk} times the column in $\mathbf{S}$ assigned to species s. This expansion results in the $E \times n_k$ matrix of individual mean responses $\tilde{\mathbf{S}}_k$. There is a k subscript only because the numbers and species identities of individuals at each site differ; we retain the assumption that individuals share the same species-level responses to the environment, regardless of where they occur. With this shift from species to individuals, response $\mathbf{h}_k$ in eq. SK is now a length-n_k vector.

There is an equivalent translation for the covariance model in eq. SU, from $S \times S$ species covariance $\mathbf{C}$ to $n_k \times n_k$ individual covariance $\tilde{\mathbf{C}}_k$ (Appendix). This individual covariance matrix has a block structure, where each block holds the covariance $\mathbf{C}_{ss'}$ between two species s and s' within a $n_{sk} \times n_{s'k}$ submatrix. Again, $\tilde{\mathbf{C}}_k$ has a location subscript only because the numbers of individuals of each species vary by location. As before, covariances between individuals of any two species depend on species identity, regardless of where those individuals occur.

Both ways of organizing environmental responses are needed to understand the relationship between coexistence and the individual covariances that can be observed in field data. The structured-known (eq. SK) model describes species differences in terms of their responses to the environment. The SK model describes *why* competition is concentrated within the species. By shifting the mean differences to the covariance between indviduals, the structured-unknown (eq. SU) representation exposes the fingerprint of this process. This translation to observable variation suggests models that can generate diversity: everything about species responses to the environment that affect competition is contained in the covariance between individuals. For completeness, the unstructured-unknown (eq. UU) variation is included as a link to literature that considers effects of adding noise to a mean parameter value for a species s (held in a vector $\mathbf{s}$) contributes to coexistence (Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019),

$$h_{isk} \sim N(b_s, c_k + \tau^2) \tag{UU}$$

The variance term c_k is included to assure that the SU and UU models are compared for the same overall variance levels. The three models are used with the same assumptions about local, crowding-driven mortality and dispersal between sites (Appendix).

Simulation demonstrates that structured variation of either type (eqs. SK, SU) allows for diverse communities, provided that the environment offers many ways for species to differ (large E in Fig. 24a, b). Large E means that not only is there high dimensional variation in the environment, but also that species are capable of responding to it. As E increases, both diversity and richness increase (Fig. 24a, b). Despite identical distributions for individual differences on the continuous scale, simulated diversity in the SK and SU cases is not precisely the same due to discretization of birth, survival, and dispersal on small plots where one model responds to the local environment (SK) and the other does not (SU) (Appendix).

III. How and why?

How does the model generate diversity and, more paradoxically, why do the differences in SK translate to the SU model, where competition is solely regulated by individual covariance? The SK outcomes can be examined on a suitability map constructed from the known environment and species responses $\mathbf{K} = \mathbf{ES}$ (shading in Fig. 24e). In simulation, the dominant individuals are expected to belong to the species having the highest performance for that site. Indeed, these are the dominant species, shown as outlined cells in Fig. 24e, with one highlighted cell per row (per site). There is not only alignment of these dominant site-species combinations; there is also positive correlation between species local responses (elements of matrix $\mathbf{K}$) and species abundance in simulation, termed "site sorting" in Fig. 24c. This site-sorting is actually stronger than it appears due to the fact that the correlations are degraded in Fig. 24c by the zeros for all local extinctions in simulation.

The SU model confirms that coexistence comes from concentrating competition within species, and, less intuitively, why it only happens if there is high dimensional variation in the environment. Demonstrating that coexistence occurs when every species is allowed to dominate somewhere is not new. However, the mechanism here differs from previous models, being based on high-dimensional species differences that incrementally increase overlap between similar individuals, while offering ways to incrementally diverge from dissimilar individuals. When E is large, the most similar individuals tend to be those of the same species. The mechanism does not involve parameter tradeoffs.

By analogy with Lotka-Volterra, which requires diagonal dominance in the interaction matrix, coexistence here comes with diagonal dominance in $\mathbf{C}$, which confers the tendency of individuals to respond more like others of the same species. When the environment is simple ($E = 2$ in Fig. 24f), there is no tendency for diagonal dominance–the covariances between individuals of the same species are rarely the largest pairwise covariances. A low-dimensional environment imposes weak covariance held in a matrix where the most similar responses, and thus, the strongest competition, often comes between individuals belonging to different species. A simple environment offers few ways in which species can differ and, thus, cannot focus competition within the species.

Diagonal dominance in $\mathbf{C}$ emerges as the environment becomes complex. This is an inevitable result of the many ways that an individual can respond to variation, increasing the dimensions in which it aligns with others of the same species and differs from individuals of other species. With E as small as 20, the shift toward diagonal dominance is already apparent (Fig. 24g). In the SK model, species differences come through their similar mean responses (matrix $\mathbf{S}$). In the SU model, these differences are transferred to the covariance (matrix $\mathbf{C}$). Either way, the covariances between individuals are the same, in both cases induced by $\mathbf{ES}$. The cumulative increase in confrontation between individuals of similar species occurs on sites where they are favored (SK model). Or it occurs without any reference to the site conditions, but it is observable in the covariances between individual responses (SU model). The species covariance $\mathbf{C}$ becomes a substitute, albeit degraded, for the information held in $\mathbf{ES}$ that cannot be observed. These similarities are the basis for competition, *i.e.*, niche overlap. The important role of the SU model is the link it provides to variation that can be observed in data, the matrix $\tilde{\mathbf{C}}$.

Without variable responses to a variable environmental ($E = 1$), diversity in the UU model reduces to the species that dominates on average (UU in Fig. 24a, b). Variation of the UU model type can have effects that depend on specific model assumptions (Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019). Models that increase variance with the introduction of noise to an individual demographic rate increase the tendency to "drift", as randomly assigning advantages and disadvantages to each individual (and, thus, species) amounts to guaranteeing that members of each species can win somewhere. Our model does not confound individual variation with total variation, because we use c_k to equalize total variation in eq. UU (Appendix).

IV. Process to data

If high-dimensional variation between species, a tiny fraction of which is represented by leaf shape (Fig. 23), evolves by natural selection (not all of it does), then this variation has to affect demographic rates in ways that affect fitness. If this has to be true, how does natural selection act on the variation that is rarely evident in estimated demographic rates? Demographic studies commonly find few significant predictors in noisy data and broad overlap between species parameters (Clark et al. 2014; Kunstler et al. 2021). The typical sample size for demographic estimates can range from tens to thousands of individuals of a given species. Most include a small number of sample dates (van Mantgem et al. 2009; Stanke et al. 2021; Qiu et al. 2021; Kunstler et al. 2021). Finding significant relationships in noisy data from limited sites and few time intervals is challenging (Tang et al., in review). By contrast, natural selection can operate every year over generations on variation across individuals spanning entire regions, especially where pollen and/or seed dispersal is high (Ashley 2010; Smith et al. 2020; Kling and Ackerly 2021; Dering et al. 2021).

The high-dimensional variation that promotes coexistence in this study makes noisy demographic rates inevitable. To see this, consider that species covariance $\mathbf{C}$ scales with environmental dimension E. As a transparent illustration, consider the case where both the columns in $\mathbf{E}$ and the rows in $\mathbf{S}$ are centered, and columns in $\mathbf{E}$ are standardized to unit variance. This centered, standardized version of the model exposes the direct scaling between residual covariance and environmental complexity, with $\mathbf{C}$ tending to $E \times Cov(\mathbf{S})$ with increasing E. A typical demographic study might benefit from up to 10 predictors, while responses occur in hundreds of dimensions. Where coexistence depends on large E, demographic rates will necessarily be poorly explained by the variables that can be measured.

V. Hybrid solution to model diversity

Demonstrating that covariance structure observed in nature can stand in for the species differences that regulate diversity offers a new direction for development of models for global change. Earth system models for this purpose must continue to strive for the relationships that describe real-world responses, without biases that might be imposed simply to guarantee coexistence (*e.g.*, tradeoffs that are not found in data or unrestricted seed availability). The need to incorporate what is known in the mean structure of a model with new understanding of how observed covariance can stabilize coexistence in such models suggests a hybrid approach.

Rather than an omnibus algorithm, the universal coexistence hypothesis offers a strategy for model development that is adaptable. Stand simulators and earth surface models include parameters that describe responses from xylem architecture, chloroplasts, and stomata to leaves to individual birth and death to canopies. The covariance important for coexistence in a model depends on the level at which competition occurs, which can be individuals, species, cohorts, or functional types. The ways in which parameters at one scale induce covariance at another will likewise vary between models.

A hybrid strategy for the model used here (individual trees that covary in demographic rates like Clark 2010) integrates the estimates of observable effects together with residual variance (eq. SK),

$$\mathbf{h}_k \sim MVN(\mathbf{b} + \tilde{\mathbf{S}}'\mathbf{E}_k, \tilde{\mathbf{C}}_k + \tau^2\mathbf{I}_{n_k}) \tag{HY}$$

The residual covariance in eq. HY allows for the unmeasurable variables that contribute to species differences, beyond those that enter through measured variables. In this hybrid, rows in $\tilde{\mathbf{S}}$ only include variables that can be observed, while $\tilde{\mathbf{C}}$ includes the unobservable sources of covariance. This hybrid remains fully consistent with both the SK and SU models, but it exploits information that can be observed for both mean and covariance. Options for this implementation include an approach summarized in Box 1.

VI. Universal application

Recent evidence that intra-specific competition in forests may be stronger than inter-specific competition (Harms et al. 2000; Wills et al. 2006; Bagchi et al. 2014; Zhu et al. 2015; LaManna et al. 2017; Hülsmann and Hartig 2018) is expected from the universal coexistence hypothesis, but it is attributed in the literature to a different cause. The Janzen-Connell (JC) effect (Janzen 1970; Connell 1971) requires that any abundant species will suffer increased losses to host-specific natural enemies, disproportionate to its less abundant neighbors. While this effect would certainly contribute to diversity, the requirement for as many host-specific enemies as there are competing host species may not be widely applicable (Novotny et al. 2006). As with efforts to achieve coexistence in competition models by imposing tight tradeoffs, the many host-specific natural enemies needed for JC lacks the empirical support that already exists for the universal coexistence hypothesis (Clark 2010), which has the further advantage that it does not depend on assumptions that may lack generality.

Continuing efforts to understand coexistence and anticipate biodiversity loss have to start by resolving what has become a 50-year impasse: how to generate diversity in models of intense competition for apparently few limiting resources. The ubiquitous requirement for tradeoffs in models (Tilman 2011) must confront the long (and still growing) legacy of demographic studies that do not support the existence of these tradeoffs (Clark 2010; Clark et al. 2018). From the earliest stand simulators (reviewed in Shugart 2003) through recent efforts (Rüger et al. 2020), models using estimates that find support in field data have resorted to immigration from elsewhere to stave off the extinction of all but a few species. The universal coexistence hypothesis resolves the paradox of widely appreciated species differences that must contribution to biodiversity, while having few observable effects on demographic data. Coexistence of competitors need not appeal to carefully specified tradeoffs for the same reason that real communities are invaded repeatedly–if many variables contribute to population success, then universal coexistence is nearly automatic; individuals typically respond more like other individuals of the same species, thus concentrating competition within the species. Individual differences observable as covariance structure can guide future modeling efforts needed to maintain realistic diversity without abandoning realistic assumptions or the evidence in data.

Acknowledgements

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Box 1: Broad implementation

The goal of a hybrid model is to permit simulation based on parameters fitted to data, while exploiting residual covariance that promotes diversity. Direct model fitting to individual responses will generally not be feasible, because it requires a positive-definite covariance among individuals. A positive-definite covariance matrix on 10 individuals would require more than 10 years of measurements. The species covariance matrix in eq. SU contains two terms, $\mathbf{C} = \mathbf{S}'\mathbf{V}_{\mathbf{E}}\mathbf{S} + \tau^2\mathbf{I}_S$. The first term is positive definite if the inner product E is at least as large as the number of species. This result has direct analogy to MacArthur's analysis of the species interaction matrix (MacArthur 1969; Advani et al. 2018), where E would represent instead the number of resources. However, matrix $\mathbf{C}$ can be positive-definite even if the first term is not, due to the second term, which acts like the nugget in geospatial models. Either way, we cannot fit (and do not want) the $n(n-1)/2$ coefficients that would be needed to fill a covariance matrix between n individuals. As in Clark (2010), the species covariance matrix here will be built from mean correlations between individuals.

Implementation would differ for each model; here we consider a case where demographic rates (*e.g.*, growth, fecundity) are fitted to j observations on individuals i across monitoring plots k. Fitted estimates constitute the mean structure that will be used to assemble $\tilde{\mathbf{S}}$ in eq. HY. We want to replace the residual (unexplained) variance from this fitted model with a covariance that will have to come from correlation of residual variation between individuals. For a normal or log-normal case, there is a likelihood

$$[\boldsymbol{\beta}_s, \sigma_s^2] \propto \Pi_{i,j} N(g_{s,i,j,k}|\mathbf{x}_k'\boldsymbol{\beta}_s, \sigma_s^2) \tag{3.1}$$

for predictors in the vector $\mathbf{x}_k$, responses for species s in coefficient vector $\boldsymbol{\beta}_s$, and residual (unstructured) variance σ_s^2. Because the individual covariance is unavailable, we wish to approximate its influence where fitted parameters are used in simulation. In the following steps, $(\hat{\boldsymbol{\beta}}_s, \hat{\sigma}^2)$ are estimates from the fitted model (eq. 3.1):

1. Concatenate the $\mathbf{x}_k$ vectors as rows to produce environment × predictor matrix $\mathbf{E}$ (eq. SK).

2. Concatenate the fitted $\hat{\boldsymbol{\beta}}_s$ coefficient vectors for each species as columns to produce predictor × species matrix $\mathbf{S}$ (eq. SK).

3. The covariance matrix needed here satisfies $\mathbf{C} = diag(\hat{\boldsymbol{\sigma}})\hat{\mathbf{R}}diag(\hat{\boldsymbol{\sigma}})$, where $\hat{\boldsymbol{\sigma}}$ is a vector of the residual standard deviations from the model fitted to each species (eq. 3.1), and $\tilde{\mathbf{R}}$ is the matrix of mean pairwise residual correlations as in Clark 2010. Note that this covariance conserves the total variance in the data. This matrix is constructed using the residuals from the fitted model, $r_{i[s,k],j} = g_{i[s,k],j} - \hat{g}_{i[s,k],j}$, which are then correlated between all individual pairs that occur at the same site k, $\rho_{i[s],i'[s'],k} = Cor(r_{i[s,k],j}, r_{i'[s',k],j})$. These correlations are averaged over individual pairs and locations to generate mean correlations $\bar{r}_{s,s'} = E_{ii',k}\left[\rho_{i[s],i'[s'],k}\right]$ for each species pair. These are the elements of matrix $\hat{\mathbf{R}}$.

4. For simulation, expand species responses $\mathbf{S}$ and covariances $\mathbf{C}$ to individual $\tilde{\mathbf{S}}_k$ and $\tilde{\mathbf{C}}_k$. For example, let $c_{s,s'}$ be an element of $\mathbf{C}$ obtained in the previous step. Upon expansion,

covariances between individuals are organized in the $n_{k,t} \times n_{k,t}$ matrix

$$\tilde{\mathbf{C}}_{k,t} = \begin{bmatrix} \mathbf{C}_{1,1} & \dots & \mathbf{C}_{1,S} \\ \vdots & \ddots & \vdots \\ \mathbf{C}_{S,1} & \dots & \mathbf{C}_{S,S} \end{bmatrix} \tag{3.2}$$

where $\mathbf{C}_{s,s} = c_{s,s} + \tau^2 \mathbf{I}_{n_{ks,t}}$ is the block for individuals of species s, and $\mathbf{C}_{s,s'} = \mathbf{1}_{n_{ks,t}} c_{s,s'} \mathbf{1}'_{n_{ks',t}}$ is the off-diagonal $n_{ks,t} \times n_{ks',t}$ block for individuals of species s and s'. Even with concentration of variance in the diagonal blocks (*i.e.*, within the species), τ^2 is needed to insure that $\tilde{\mathbf{C}}$ is positive definite, because, among other things, the entire diagonal block $\mathbf{C}_{s,s}$ holds the same value $c_{s,s}$.

Although the description here uses the same sites for model fitting as for prediction, $\mathbf{E}$ could also come from other locations. A typical inventory study would have access to pairwise covariances between individuals that can be estimated for time series of limited duration (Clark 2010).

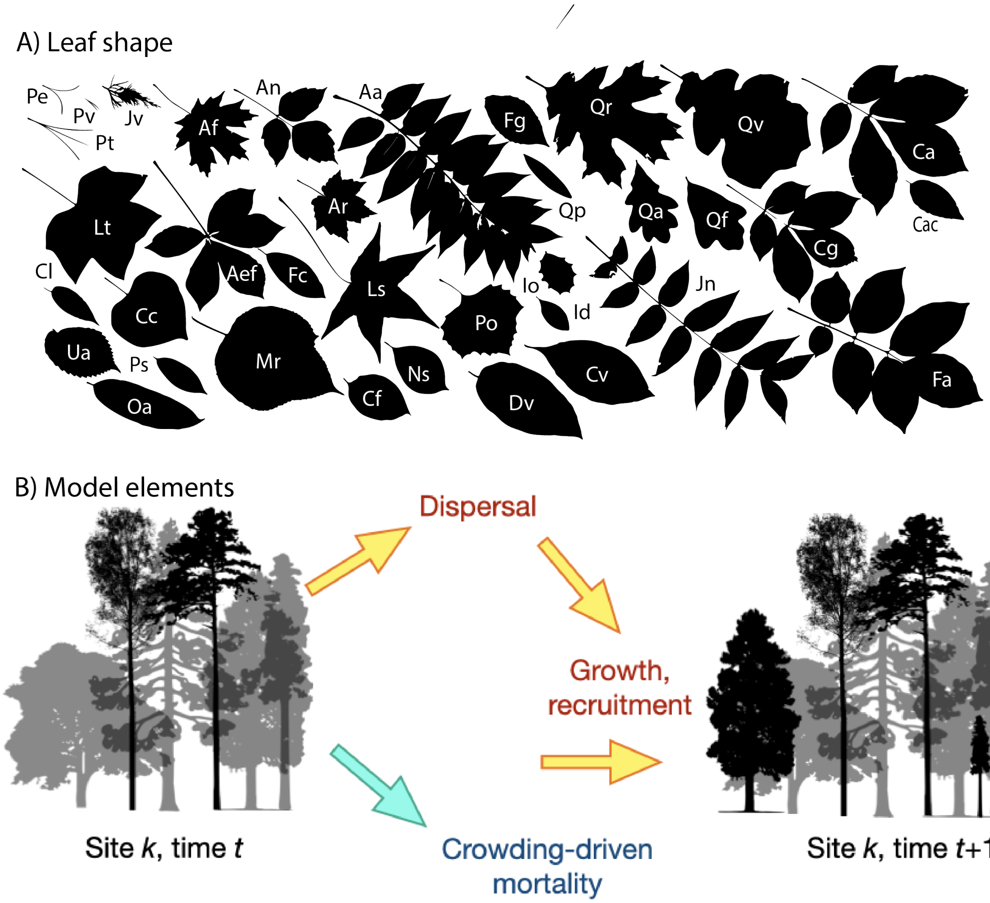

Figure 23: A) Leaf shape is an example trait that varies widely within a single forest. Here is presented a subset of the variation (34 of 59 tree species) from a temperate forest. If evolved by natural selection, then this variation must affect fitness and, therefore, demographic rates. B) The model allows for high-dimensional variation in the environment and species responses (see text), partitioned as reproduction, mortality, and dispersal. Acronyms in (A) are for *Acer floridanum*, *A. negundo*, *A. rubrum*, *Aesculus flava*, *Ailanthus altissima*, *Carpinus caroliniana*, *Carya alba*, *C. glabra*, *Celtis laevigata*, *Cercis canadensis*, *Chionanthus virginiana*, *Diospyros virginiana*, *Fagus grandifolia*, *Frangula caroliniana*, *Ilex decidua*, *I. opaca*, *Juglans nigra*, *Juniperus virginiana*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Morus rubra*, *Nyssa sylvatica*, *Oxydendron arboreum*, *Pinus echinata*, *P. taeda*, *P. virginiana*, *Platanus occidentalis*, *Prunus serotina*, *Quercus alba*, *Q. falcata*, *Q. phellos*, *Q. rubrum*, *Q. velutina*, *Ulmus americana*. Photos by Samantha Sutton.

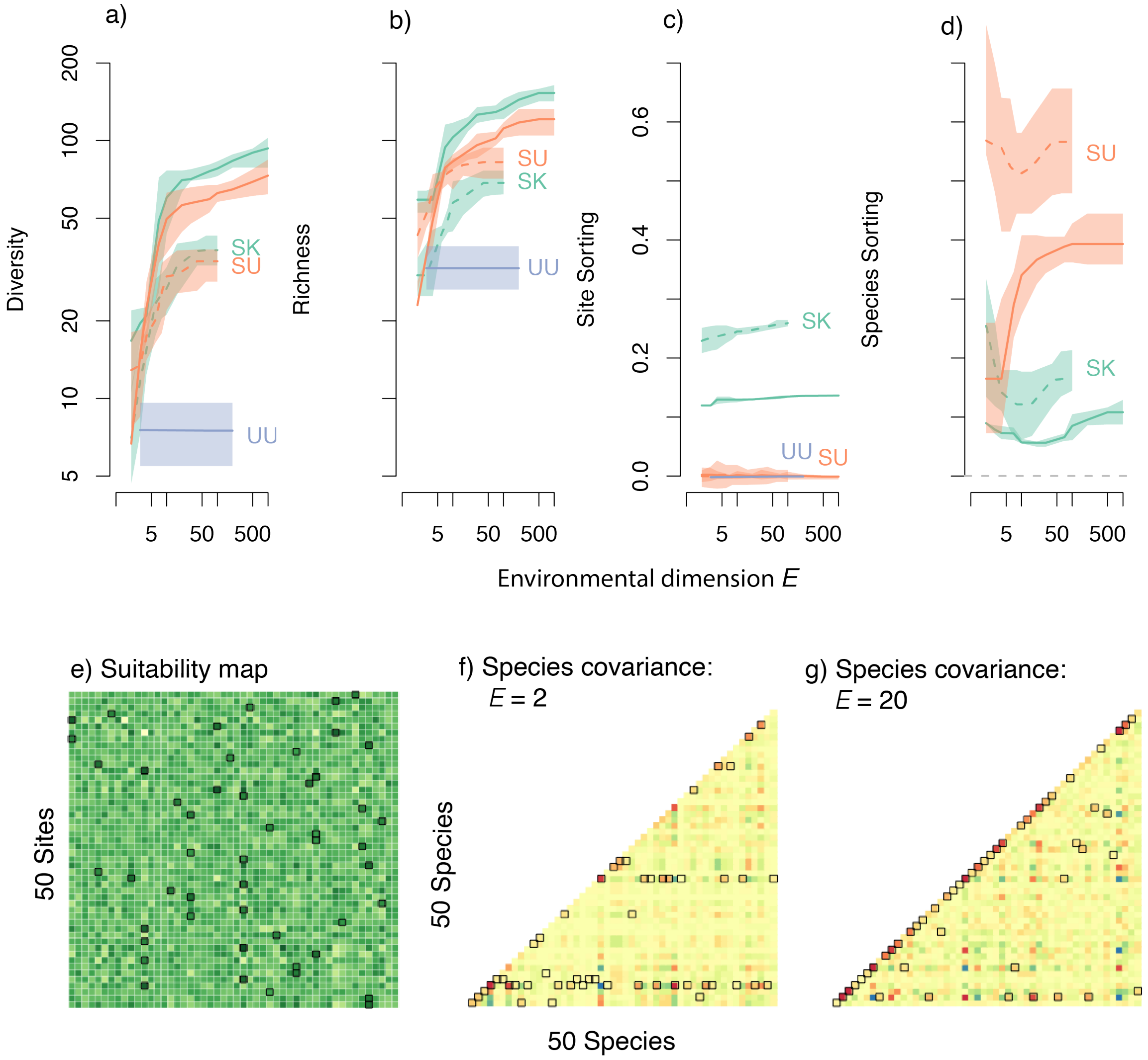

Figure 24: Dimensionality E and coexistence for the structured-known SK, structured-unknown SU, and unstructured UU models. Each model is shown for parameter sets on small (dashed lines, $K = 50$) and a somewhat larger (solid lines, $K = 500$) landscape (Table 15). Species **diversity (a)** and **richness (b)** are Shannon entropy and number of species, respectively. **Site sorting (c)** shows the correlation between species abundance in simulation and the underlying suitability of the landscape, $\mathbf{K} = \mathbf{ES}$, which is shown as a suitability map in **(e)** (dark shading indicates high suitability for a location/species combination). Bounding boxes in **(e)** indicate the dominant species in simulation (one box per row). **Species sorting (d)** is the correlation between species covariances in simulation and the covariance induced by their differing responses in matrix **C (f, g)**: the largest species covariance pair in each column of **f, g** is highlighted with a bounding box (color ramp from negative blue to positive red). Diversity shifts from **(f)** a simple environment ($E = 2$), where a few species dominate to **(g)** strong diagonal dominance expected where responses depend on a number of variables ($E = 20$). The effect of this shift is the increase in diversity with increasing E in **a, b**. Parameter values are given in Table 15.

General discussion

I. Synthesis

The main goal of the thesis was to present and test hypotheses on an alternative view of intraspecific variability in ecology, which is often approached as a noise around species mean attributes that makes species more similar. To do so, we adopted several approaches, from simple theoretical illustration to forest data analysis and community dynamics models.

In the first chapter, we first provided a pedagogical illustration to show how a large intraspecific observed variability can emerge from mischaracterised environmental variation, here consisting of unobserved dimensions of the environment. An important aspect of this analysis is that it is not a proof that this is the case, but rather that it is possible, in accordance with the well-known fact that individuals respond to the environment thanks to phenotypic plasticity; this approach is not an evidence that this process operates in data, but rather an illustration of how it could occur. Therefore, this illustration should not be considered alone, but concomitantly with the data analyses presented in the same chapter. To test whether observed intraspecific variability, or at least a part of it, result from mischaracterised environmental variation in real communities, we then first moved to a conservative, highly-controlled, experimental set-up where environmental variability was minimised and genetical intraspecific variability was controlled. More specifically, we tested if intraspecific variability could be observed in growth within Eucalyptus tree clones residing in the same plots. As it was the case, and as abundant literature on $G \times E$ interactions in common gardens shows that heritability is always lower than one, this provides experimental evidence that not purely genetic sources of variation leads to observed intraspecific variability. However, these sources can be of various kinds (although they could be considered as part of the micro-habitat): initial manipulations of seedlings, within-plot environmental variations, subsequent effect of asymmetric competition, *etc.*, therefore more specific experiments with fine-scale environmental monitoring could help quantifying the relative effects of different non-genetic sources of intraspecific variability. We finally moved to tropical forest communities to test whether natural plant communities, and especially hyperdiverse ones, also hold the signature of this view of intraspecific variability. More specifically, we tested whether intraspecific variability in tree growth was spatially-structured, which would not be the case for a purely random intraspecific variability, in three contrasting tropical forest datasets. After confirming that observed intraspecific variability in growth was high even after accounting for the effect of diameter, we showed that growth was spatially autocorrelated within a 100-m radius, even without accounting for the effect of diameter nor ontogeny. We interpreted this as the signature of environmental drivers of growth, which are spatially autocorrelated. However, we acknowledge that spatial autocorrelation could also emerge from genetic patterns for instance due to local adaptation or limited dispersal. Here again, more tests are required to better distinguish the sources of intraspecific variability. Lastly, we showed that growth was more similar within conspecific than heterospecific individuals. Therefore, in those tropical forest datasets, the high observed intraspecific variability does not prevent species from responding differently to environmental factors. A part of observed individual variability is not a coexistence mechanism but is the signature of the response of species to a high-dimensional environment varying in space and time. Overall, this chapter provides complementary approaches to invite to a renewed perspective on intraspecific variability, its sources, its structure and its consequences on coexistence.

Analyses in Chapter 1 overall led to the conclusion that the widely used way to represent intraspecific variability in models - as a random noise without any structure - does not represent well the intraspecific variability observed in the data, with potential consequences on simulated community assembly. Indeed, while a random noise would lead to a niche overlap, it is not the case of the response of individuals to different environmental stimuli. In Chapter 2, we thus develop further the simple theoretical model used in Chapter 1 in order to clearly test the effect of substituting structured and environmentally-driven intraspecific variability by a random noise on community dynamics. In other words, we tested the hypothesis that the way intraspecific variability is introduced in community dynamics models matters. To do so, we designed a simulation experiment where we introduced three different performance models in the same community dynamics simulator in order to compare the outcomes. The first performance model was a "perfect knowledge model" that could represent a hypothetical reality, where all determinants of performance (*i.e.* environmental variables and species-specific responses to them) are known. We then mimicked the imperfect perception of reality by ecologists by inferring species-specific parameters knowing individual performances (computed using the perfect knowledge model) and only some of the environmental variables that actually determine performance. The proportion of knowledge varied from 0 to 100%. For each species, the variability in performance that was not explained by the observed environmental variables was considered as an unstructured intraspecific variability. The second and third performance models were "imperfect knowledge models" without and with unstructured intraspecific variability respectively. Those models computed performance using the observed environmental variables and the corresponding previously inferred species-specific parameters. A species-specific unstructured noise (*i.e.* the unexplained variability) was added to the computed performance for the third model only. Therefore, the perfect knowledge and the imperfect knowledge models with unstructured intraspecific variability shared the same amount of variation in performance, but this variation was structured differently. Comparing the outcomes of the simulations of these models enabled to test the effect of substituting a structured and environmentally-driven intraspecific variability with an unstructured random noise. Comparing the imperfect knowledge models with and without unstructured intraspecific variability with the same number of observed dimensions enabled to evaluate the benefits of introducing intraspecific variability in a unstructured way *vs.* ignoring intraspecific variability. The main results were that i) communities simulated with unstructured intraspecific variability never reached the community diversity and composition of those where all the variation was explained and structured (perfect knowledge model), highlighting that incorporating unstructured intraspecific variability to account for unexplained (but structured) variation can be misleading; and ii) the effects of incorporating unstructured intraspecific variability depended on the relative importance of structured *vs.* unstructured intraspecific variability (*i.e.* the proportion of knowledge). In particular, increasing the proportion of unstructured intraspecific variability into the model moved from a positive to a negative effect on community diversity and similarity in composition with the communities obtained using the perfect knowledge model. A complementary result was that coexistence in these simulations were enabled thanks to a) species differences and b) environmental variation in many dimensions, which together enabled each species to perform best somewhere in the landscape. The main results of this chapter overal suggest that it is crucial to account for the sources and structure of observed intraspecific variability in real communities to better understand its effect on community assembly and properly include it in community dynamics models.

In Chapter 1, we showed that a part of observed intraspecific variability was not due to differences between conspecific individuals that would impact species coexistence, but was rather the signature of the response of species to high-dimensional environmental variations. This leads to wonder what mechanisms could enable (i) to observe a high intraspecific variability in data (ii) to enable species coexistence. In Chapter 2, we showed that this could be achieved through species differences combined with environmental variation in many dimensions. Moreover, this experiment led to the conclusion that the standard way to introduce intraspecific variability into community dynamics models, namely a random, unstructured noise, was not appropriate in most situations. We therefore recommended to introduce the structure of intraspecific variability in models. However, both achieving coexistence thanks to high-dimensional environmental variation and introducing the structure due to environmental variation in models require an excellent knowledge of environmental factors, which is rarely available. In Chapter 3, we aimed at providing a method to do so. We thus tested whether introducing only the structure of intraspecific variability in models, *i.e.* without introducing the underlying drivers of such structure, was sufficient to generate coexistence in a community dynamics model. More specifically, we tested if the fact that all individuals are submitted to the same environmental conditions but respond more similarly within than across species leads to a stronger intra- than interspecific correlation of performance, and if this enabled species coexistence. We performed these tests at different levels of dimensionality (see below what we mean by dimensionality). We then further tested if introducing a structured covariance matrix inferred from observations in a community dynamics simulator, but without information on the drivers of this structure, enabled to reproduce community patterns such as species diversity and environmental filtering. The main results were that i) as dimensionality increases, the matrix of correlations of performance becomes diagonal dominant (*i.e.* the correlation is stronger among conspecific individuals) and ii) as dimensionality increases, coexistence is fostered. Moreover, iii) introducing structure using covariance matrices in a community dynamics model enables to reproduce some features of the community, but not all of them (*e.g.* species diversity is well reproduced but not environmental filtering). iv) In these models, observed intraspecific variability was high and structured due to environmental variation in many dimensions. These variations (together with species differences) enabled species coexistence, but intraspecific variability was not the *cause* of coexistence. v) We finally proposed a method that could include environmental knowledge as well as structured intraspecific variability due to unknown environmental variations, and which could be implemented using data from the field. We suggest that this “hybrid model” could be used to enable community dynamics models to generate the high number of coexisting species observed in the field without using fine-tuned trade-offs or seed rains.

In the next sections we discuss our choices, put these three chapters in a broader scientific context and provide perspectives.

II. Modelling choices and scientific approaches

Analyses and models presented in each chapter can be classified in respect of the scientific approaches that were adopted. Each data analysis (in Chapter 1) aimed at detecting general patterns in data, therefore following an inductive approach. This type of approach has been either promoted for ecology, or has led to questioning ecology as a science (Wilson 2003). The theoretical models that were presented (the theoretical illustration of Chapter 1 and the models of Chapters 2 and 3) aimed at testing hypotheses, and were therefore following a deductive approach. However, these tests did not consist in falsifying but rather in verifying the hypotheses. This is a potential criticism, since falsifying hypotheses is considered as the only way to scientifically test a hypothesis (Popper 1959). However, verification is broadly used in ecology since falsification is difficult (Wilson 2003), and still enables to increase knowledge (Maris et al. 2018).

In Chapters 2 and 3, what enables coexistence in the models is spatial heterogeneity coupled with niche partitioning (also called species differences *e.g.* in the title of Chapter 3); both mechanisms have been well-documented in ecology and biogeography (spatial heterogeneity: Tilman 1982; Chesson 2000a; Stein et al. 2014; niche partitioning: Gause 1934; Hutchinson 1957; Hurtt and Pacala 1995). Therefore, in both models, the mechanisms that enable coexistence are not novel. However, the fact that variation of the environment in *many* dimensions relaxes constraints for trade-offs has not been often discussed beforehand. There is no need for finely-tuned parameters to achieve coexistence here because as dimensionality increases, almost any random set of species parameters would allow the species to perform best somewhere in the landscape. In Chapter 2, we evidenced the effect of the way intraspecific variability is introduced in theoretical community dynamics models on model outcomes, including species coexistence and species abundances. In Chapter 3, we showed how the use of a structured covariance matrix in a community dynamics model enables to reproduce most properties of the actual community, even in absence of knowledge of the underlying drivers of such structure.

In order to put the community dynamics models used in Chapters 2 and 3 in a broader context of modelling literature, we use the conceptual framework proposed by Barbier (in prep), which aims at classifying conceptual explanations and mathematical models of many-species communities. This framework is organised along three main axes: randomness *vs.* simple structure, one-way causality *vs.* feedback, and stationary *vs.* transient/historical (Figure 25). The first axis could for instance represent a deterministic explanation with clear niche differences or trade-offs where the behavior of individual species are predictable *vs.* a probabilistic explanation with collective phenomena where individual species are unpredictable. In both models used in this thesis, the dynamics are mostly deterministic in the sense that species parameters are known and fixed, and determine their distribution, abundance and survival. Regarding the second axis of Barbier's framework, the one-way causality side could represent models in which species' location tracks favored environment and is mainly determined by its own features, preferences and processes, and where self control dominates. The feedback side could represent models in which species' presence strongly impacts and is impacted by other species and factors, and where other-control dominates - what is happening to other species impacts the focal species. Both models presented here rather correspond to the one-way causality side. Indeed, species are partitioning the environment and therefore do not interact, a species' location is determined by its preferences, and a species limits itself in Chapter 2 in the sense that an individual cannot occupy a favorable habitat that is already occupied by a conspecific. However, all species compete for space, which creates a feedback between species, potentially moving our models to the right, but as density-dependence is not species-specific, it does not impact coexistence. For the third axis, the transient/historical side could represent dynamics that are shaped mostly by few large (historical) events, like a massive extinction and a founding effect, and by initial conditions. The stationary side could represent dynamics that are mostly shaped by frequent, “minor” events, and where the space of possibilities is well explored. In both models presented here, although initial conditions can determine the presence or absence of a few species (*e.g.* there is variability in the community composition between initial conditions in Chapter 2), the dynamics are mostly shaped by regular death and recruitment event. Therefore, our models correspond to the stationary side of this axis. Overall, our models both stand in the left, down corner of the cube. Important aspects of ecological dynamics were therefore ignored in our framework, like feedback interactions (which would move our models to the right) or the effect of dispersal (which would move our models backward). Adding the effect of random mutations

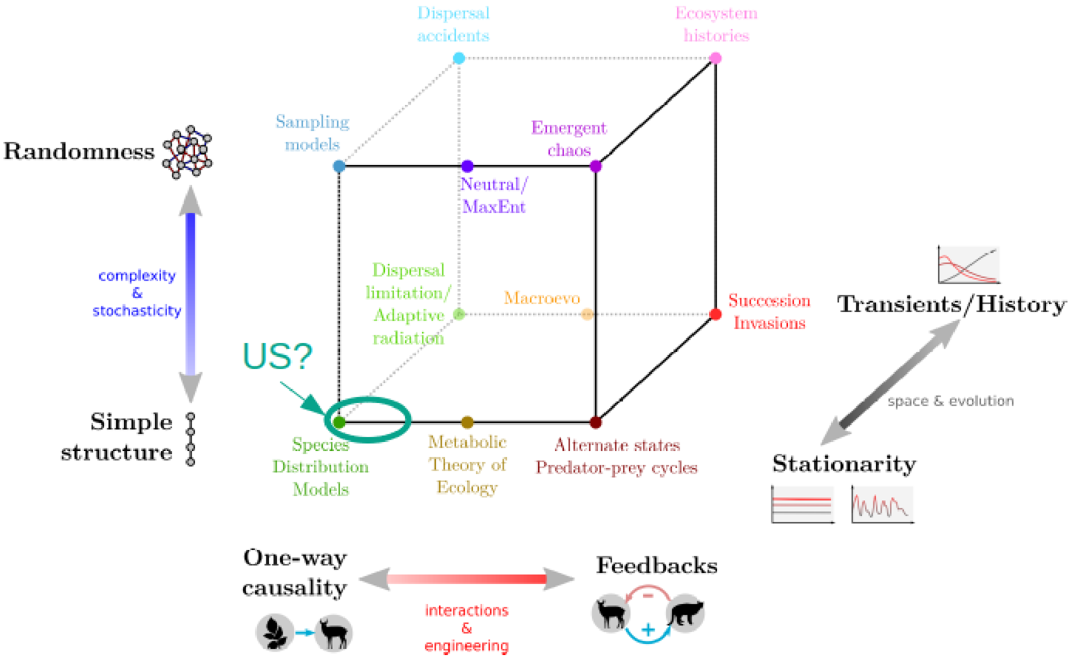

Figure 25: Replacing our models in a conceptual framework for multi-species models. Shown are the three axis proposed by Barbier to describe differences in concepts of multi-species models, with examples located on this three-dimensional volume. The models used here in Chapters 2 and 3 would locate around the green circle.

and evolution could move the model upward and backward, but they are likely to happen at longer timescales than the ecological interactions we are interested in - although we discuss the relevance of this assumption below.

III. High dimensionality and variable environment

The two necessary ingredients that enable coexistence in our framework are a "high dimensionality" and a variable environment (*e.g.* number of environmental dimensions in Chapter 2 and E in Chapter 3). In our case, coexistence could not appear with a homogeneous environment, nor if only a few resources are taken into account.

By high dimensionality, we mean two components. The first one is the high dimensionality of the environment, which encompasses resources, but also abiotic variables that are not resources like temperature, and biotic variables like the presence or abundance of natural enemies. Note that in Chapter 2, environmental variables do not change in time, therefore making them unlikely to represent dynamic environmental variables like biotic variables. Similarly, in the models of Chapters 2 and 3, the lack of feedback between the number and characteristics of individuals in the landscape on the one hand and the environmental variables on the other hand make them unlikely to represent resources that would undergo depletion as they are used by the individuals. To reference the framework of Figure 25, the environmental dimensions implemented in our models are on the "one-way causality" side of the horizontal axis.

The second component of high dimensionality is the high dimensionality of species response. Indeed, species responses to an environmental variable often cannot be described by a single parameter. Instead, many responses are non-linear, which multiplies the opportunities of each species to differ from potential competitors (Figure 26). As a consequence, while in Chapter 3

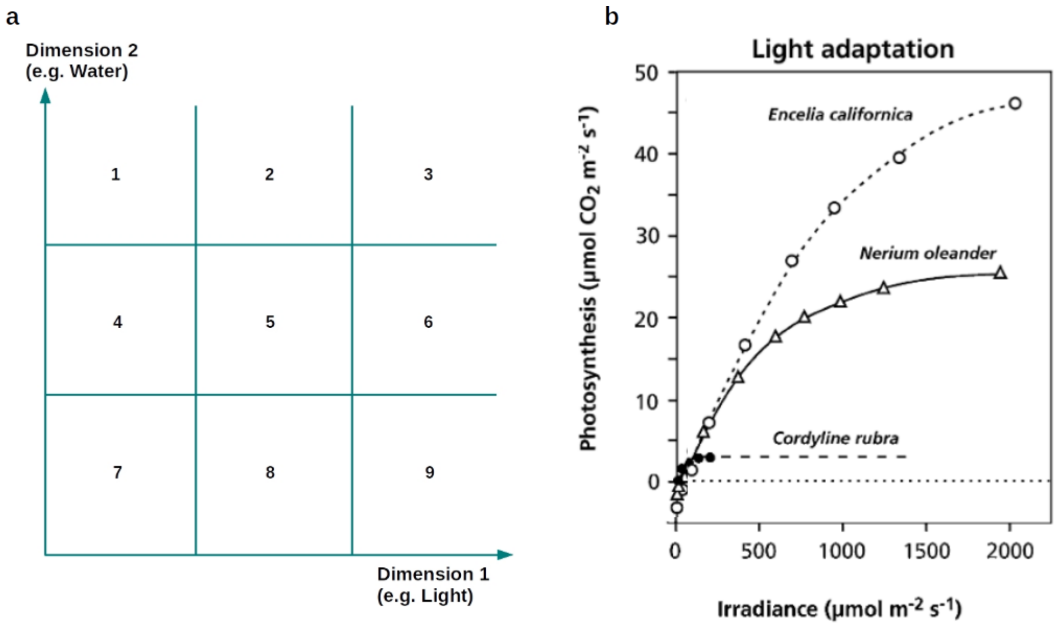

Figure 26: High dimensionality emerging even from few environmental dimensions due to non-linear species responses If the response of species to one given environmental dimension is non-linear, several parameters are needed to describe this response, leading to several dimensions in the space of species response. These can be seen as the slope of the linear approximation for each bin along the range of the environmental dimension. The more non-linear the response is, the smaller the bins need to be and the higher the dimensionality of species response is (*i.e.* there are more ways for species to differ in their response to the environment). **a.** an environment with only two dimensions where the response of species to each of these environmental dimensions is binned into three parts would result in nine ways in which species can differ in a variable environment. **b.** an example of non-linear response to environmental variation, for species which naturally occur at a high, intermediate, or low irradiance. Copyright Lambers et al. (2008). See Laughlin et al. (2012) for other examples of non-linear species responses to environmental gradients.

$E = 20$ could appear as unrealistically high, it is not the case if this is taken into account. For instance, in the case of the Janzen-Connell hypothesis, the specificity of natural enemies is not necessary in our framework; only different species responses to each natural enemy is.

Moreover, these many environmental dimensions vary in space and time at various scales as discussed in Chapter 1. In addition, temporal variation within a population can arise from processes across years (*e.g.* demographic and phenological shifts) but also within years (*e.g.* uneven age structure and phenological asynchrony) (Cope et al. 2022).

Together, high dimensionality and environmental variation enable coexistence in the models of Chapters 2 and 3. Quantifying both these elements in the field remains a challenge, although technical progress might alleviate the difficulties. In order to measure the variability of the environment, remote sensing could enable to massively acquire data with reduced costs compared to human measures in the field. However, remote sensing cannot replace some measurements like soil depth or chemical composition. One way to improve the quantification of species response would be to better characterise micro-habitats and to relate them to individual attributes.

IV. Sources of intraspecific variability: does it matter?

While it can be assumed that genetic variability and phenotypic plasticity cause similar effects in ecological communities (Violle et al. 2012), understanding if the observed intraspecific variability is heritable or not is crucial to predict global change response (Moran et al. 2016). Indeed, heritable genetic intraspecific variability impacts population-level means that are influenced by natural selection over generational timescales, while phenotypic plasticity can be an immediate response to the environment and can thus buffer rapid environmental changes, maintaining populations but also slowing down adaptive evolution (Moran et al. 2016). However, disentangling the different sources of variation can be challenging. For instance, while common garden experiments can help to distinguish genetic and plastic variability, epigenetic effects can undermine this method Moran et al. 2016), while experimentally manipulating phenotypic plasticity remains difficult (Turcotte and Levine 2016).

Moreover, intraspecific variability can also arise through plant development due to ontogeny and phenology (Cope et al. 2022)). Thus, better accounting for the effect of timing in intraspecific variability by moving away from the “snapshot approach” of intraspecific variability (which can change over time) would improve our understanding of intraspecific variability and its temporal structure. This would however require data at a finer resolution than the year, which could be feasible in some experiments but is unrealistic in the case of the majority of forest dynamics surveys. Therefore, the causes of observed variability remain unclear.

In the analyses presented here, intraspecific variability originates from the environment: in the theoretical illustration of Chapter 1 like in the community dynamics models of Chapters 2 and 3, what causes observed intraspecific variability is mischaracterised variation of the environment. However, what really matters here is the structure rather than the sources of intraspecific variability. Indeed, one could imagine that environmental dimensions in each of the models are in fact the variation in space of parameters that would vary between individuals due to genetic differences (but without heritability which is not implemented in those models). Furthermore, in Chapter 3, the main goal is to show that the diagonal dominance of the matrix of mean individual correlations enables species coexistence of a high number of species even when the causes of this diagonal dominance are unknown. Therefore, these causes could theoretically be anything, as long as they affect the performance of conspecific individuals in a more similar way than heterospecific individuals. However, in Chapter 3, the solution proposed to include structure in community dynamics models does not reproduce the effects of environmental filtering. The environmental filtering of individuals can lead species attributes to converge locally (Violle et al. 2012; Craven et al. 2018), and can lead to local adaptation (see Schmitt et al. 2020 andSchmitt et al. 2021 for the effect of topography on trait variation and local adaptation respectively). In that case, even if intraspecific variability is structured in space and time, heterospecific individuals could be locally similar. Therefore, environmental filtering could be an important feature for coexistence that is currently not taken into in our approach and could be investigated in the future.

On another note, we ignored evolutionary dynamics in our models, which is a widespread practice among ecologists. Indeed, evolutionary dynamics often happen at much longer timescales than species interactions like competitive exclusion or facilitation. However, it has been shown that those timescales sometimes overlap (Fussmann et al. 2007; Hendry and Kinnison 1999 in Bolnick et al. 2011b), making eco-evolutionary dynamics central to the understanding of communities, and intra- and interspecific diversities are expected to interact through evolution (Mougi 2020). Therefore, sources of intraspecific variability matter, not in our models where only its structure does, but in nature where eco-evolutionary feedback loops are increasingly recognised as important drivers of the dynamics, and the different sources of intraspecific variability could impact community dynamics in different ways (see above). Therefore introducing them in community dynamics models is an important endeavour.

V. Correlation, competition and coexistence: complex relationships and philosophical framework

In our framework we frequently make the link between correlation, competition and coexistence. Indeed, we hypothesized that stronger correlation in performance leads to stronger competition, and that a stronger intra- than interspecific competition leads to stable coexistence. However, each step of this argument can be discussed, and the entire theoretical framework developed here can be placed in a philosophical context.

First, a common hypothesis is that competition leads to negative correlations between species attributes in data (*e.g.* Strong et al. 1984 p.82: “If species compete, a significant negative correlation is expected.”). In the last chapter however, we showed that competing species can coexist and have positive correlations in growth rates, and a current ongoing project of the INTRACO workgroup is to test if it is the case in forest data from diverse biomes.

Second, a stronger intra- than interspecific correlation does not necessarily mean that intraspecific competition is stronger than interspecific competition. Indeed, if one interprets competition through interaction coefficients in a Lotka-Voltera model, a stronger intraspecific competition could lead to variations of attributes that are in antiphase between conspecific individuals, *i.e.* negative correlations. Therefore, clearly relating correlations between performance proxies, interaction coefficients and species coexistence would enable to consolidate our framework. As highlighted by Turcotte and Levine (2016), few studies make the link from shifts in attributes, to niche and fitness differences, to both intra- and interspecific competitive abilities. The INTRACO workgroup is currently working on relating analytically the diagonal concentration in growth correlation matrices to coexistence mechanisms in a Lotka-Volterra model. A first outcome of this work is that comparing intra- and interspecific correlations could be an interesting indicator about the relative importance of the environment *vs.* competition in shaping the community. Factors can be separated into those that species only respond to (“response factors”, *e.g.* temperature, precipitation), and those that species respond to *and* impact (“interaction factors”, *e.g.* resources, presence of pathogens or herbivores or fires) - see also the definition of the ecological niche by Chase and Leibold (2003) in the general introduction. This implies that when temporal covariation comes from the first type of factors principally, conspecifics should respond in positively correlated ways, and typically more positive than heterospecifics. On the contrary, when temporal covariation comes from the second type of factors principally, then conspecifics should respond in more negatively (or less positively) correlated ways than heterospecifics, assuming conspecifics compete more strongly with each other *i.e.* if one is doing well it impacts negatively others.

In the last chapter, all dimensions (E) correspond to response factors, and the term of density-dependence is constant across species (there is no species-specific density-dependence). This leads to a dominance of diagonal elements in the matrix of mean individual correlations. Therefore, coexistence is enabled thanks to the partitioning of the environment between species, with no feedback between the environment and the density or performance of individuals. Species basically ignore each-other thanks to spatial heterogeneity, and the strength of *realised* competition is indeed higher within than between species. However, just like the ecological niche can be thought of as fundamental and realised, so can be competition. In this model, *fundamental* competition between species is very high: if species were in the same environment, the most successful species would definitely competitively exclude all other species. Therefore, coexistence is not enabled by a higher intra- than interspecific *fundamental* competition, but only by environmental partitioning; in other words, in this model, the relative importance of intra- *vs.* interspecific *realised* competition does not matter for species coexistence. This is of utmost importance since a Lotka-Volterra derivation of this model would not lead to a diagonal concentration in the competition coefficients matrix - on the contrary. Coexistence in this model is therefore fragile in the sense that small environmental shifts could prevent it. Therefore, the theoretical discourse around this model must be pondered, and further tests should be performed. For instance, including species-specific density-dependence, feedbacks between some environmental variables and the density of individuals, and assessing the consequences on intra- *vs.* interspecific correlations would be a first step to test the relevance of this comparison to indicate the relative importance of the environment *vs.* competition in shaping the community.

Moreover, one of our objectives was to bring out a simple mechanism that would explain the common phenomenon of competitor coexistence without potentially unrealistic expectations (*e.g.* precise trade-offs, external seed rain or neutrality). This approach is in line with the desire in ecology to draw general rules, making it a "hard science" relying on a general theory like physics (a desire even referred as "physics envy", Maris et al. 2018). Hutchinson, MacArthur and other authors were the initiators of this effort of generality in ecology, with a focus on competition for limited resources as the main driver of ecological dynamics, thus ignoring "historical details" and focusing on the study of equilibria using mathematical tools (Maris et al. 2018). However, contingent events and evolutionary history are pervasive and of great importance in ecology, for instance with prior effects. Other authors consequently warned that "ecologists should resist the lure of general rules" and that ecology should address evolutionary history as well as the effect of stochastic events. As we propose a renewed link between intraspecific variability and the framework of the high-dimensional (Hutchinsonian) niche, we adopt a deterministic view of intraspecific variability that is not a scientific consensus. This thesis is thus part of a scientific debate that borders on a philosophical controversy (see the different views about the coexistence theory in the introduction).

Finally, this work falls within a philosophical context. Indeed, we here focused on the individual level and on competition as the relevant level and the main driver of community dynamics respectively, which is in accordance with the liberal ideology that currently dominates human societies. However, it is important to acknowledge that these views are not obvious and rely on strong hypotheses that are often internalised by ecologists and evolutionary ecologists. Just like any other scientific field, ecology is influenced by philosophical ideas and ideologies (Rubio 2019); other frames of mind exist when investigating the evolution and the functioning of ecosystem (*e.g.* Axelrod and Hamilton 1981 and the evolution of cooperation). The ideas developed in this thesis should therefore be thought of as an invitation to have a renewed look on intraspecific variability, and put back in this philosophical context, rather than as a standalone solution to the coexistence paradox.

VI. Perspectives

The work presented in this thesis is mostly theoretical, with few tests in data, and tests performed through verification rather than falsification. This could therefore be another case of theoretical community ecologists developing "toy models" that are difficult to relate to particular communities (Purves and Vanderwel 2014). However, "understanding and incorporating variation in traits is [...] important for basic science, for making predictions about climate change impacts, and for managing species affected by global change" (Moran et al. 2016). While the work presented here indeed focuses on theory, it also offers concrete perspectives, both to better understand the nature and the structure of intraspecific variability and to incorporate it better in forest dynamics models, which can then for instance be the basis to make predictions under scenarios and provide recommendations to hopefully mitigate climate change and biodiversity loss.

VI.1. Test of the structure in data

We propose to test (or to test further) in data the hypotheses theoretically developed in the different chapters, which would validate (or invalidate) our hypotheses. We thus propose to make corroborative-predictions, which is a necessary step of knowledge-building (Maris et al. 2018).

In the first chapter, we have shown that individual growth presents a spatial structure in several tropical forest datasets. Growth is also known to be structured in time (across "good" and "bad" years and seasons for instance). A next step would be to test if those spatial and temporal structures also exist in other datasets (*e.g.* Bebber et al. 2002 in Borneo), across different biomes (*e.g.* García 2006 in Canada) and using other attributes than growth like fecundity (Clark et al. 2021) or response functional traits. As spatial patterns like seed dispersal can have important consequences on species coexistence (Wiegand et al. 2021), relating the structure in observed species attributes to seed dispersal patterns (Nathan and Muller-Landau 2000; McFadden et al. 2019; Clark et al. 2018), genetics (Epperson 1992) or environmental variables (Nicotra et al. 1999; Bebber et al. 2002 for light) could help to better understand the sources of intraspecific variability and its consequences on coexistence.

In the last chapter, we have shown that coexistence can be allowed thanks to species differences in many dimensions combined to environmental variation. The fingerprint of this mechanism was that correlations were higher within than across species. However, this theoretical result still has little empirical support, apart from Clark (2010) that brought out this pattern in Northern American forests. It would therefore be relevant to reproduce this analysis in a diversity of communities from several biomes (*e.g.* tropical and temperate forests, grasslands). This is currently being tested by the INTRACO work group, and the preliminary results are consistent with our hypotheses. Other subtle patterns indicating high-dimensional coexistence could also be explored in data (Barbier et al. 2021).

VI.2. Introduction of structure in community dynamics simulators

If these structures are highlighted in data, a next step will be to include them in community dynamics simulators. Doing so would enable to make anticipatory-predictions, which is useful to explore possible futures and help decision-making (Maris et al. 2018). The effect of adding dimensions of environmental variation on species coexistence has rarely been explored using forest stand models. In spatially-explicit forest models (*e.g.* Courbaud et al. 2015; Maréchaux and Chave 2017), investigating the effect of adding environmental variables on coexistence would be possible but would need accurate data as well as development effort to model the interaction between variables and plants (as is currently the case to implement the water cycle in addition to light in TROLL model, Maréchaux and Chave 2017). In the Perfect Plasticity Approximation model, which is not spatially explicit, spatial structure was introduced using several simulated patches, which led to a higher coexistence (Purves and Vanderwel 2014). Another way to introduce spatial and temporal structures in community dynamics models could be to use individual random effects and temporal random effects. To inform on the underlying structure of the environment, individual random effects should be inferred from data and the location of each individual should be observed. In the absence of such data, individual effects could be distributed in space with spatial autocorrelation so that individuals are locally similar. Besides, comparison with a spatial distribution of individual effects without spatial autocorrelation could be an additional test (does spatial autocorrelation increase the number of coexisting species even when its causes are unknown?). Alternatively, a structured covariance matrix could be introduced in simulators as proposed with the "hybrid model" presented in the Chapter 3. As shown in this study, introducing structure via a covariance matrix could enable to increase the realism of simulated communities in terms of species diversity and abundances, although it fails at reproducing the consequences of environmental filtering. An interesting additional test would be to investigate if the inclusion of additional dimensions in models (Falster et al. 2017; Rüger et al. 2020) led to a concentration of the correlations of performance proxies within species and to species coexistence (it is the case in Falster et al. 2017). Better accounting for the effects of ontogeny and phenology in models could also structure intraspecific variability in time (Cope et al. 2022)). Evaluating the consequences of including structure in different simulators, especially the consequences on species coexistence, as well as the validation of the outputs using observed data will inform on the relevance of using these methods in forest dynamics models. If it increases the realism of simulation outputs, a next step would be to adapt these methods to DGVMs that are notably used by IPCC and IPBES (IPBES 2016), thus helping to project the consequences of climate change on biodiversity under different scenarii, therefore providing insights to decision makers.

VII. Conclusion

In the context of the still incompletely solved coexistence conundrum, intraspecific variability has been seen as a potential lever to move forward. Its effect on species coexistence was therefore investigated, mainly using theoretical community dynamics models that have led to contradictory conclusions. In those theoretical models, intraspecific variability has almost systematically been introduced as a random noise that made species more similar. In this thesis, we explored another view of the intraspecific variability that is largely observed in data, by suggesting that it can be the consequence of species-specific responses to mischaracterised environmental variations in many dimensions. We thus placed intraspecific variability in the framework of the high-dimensional niche (and therefore in a specific scientific and philosophical context), where both the environment and the response of species to it can contribute to high-dimensionality. To do so, we used complementary approaches, from the simple theoretical proof of concept, to experimental clonal data and forest inventory data analyses, to simulation experiments. In doing so, we adopted both inductive and deductive scientific methods, and tested our hypotheses through verification. By highlighting the importance of the structure of intraspecific variability for coexistence and community dynamics, we attempted to trigger a renewed way to consider and represent observed intraspecific variability in community ecology. The models presented here are of course wrong - as any model is - because they rely on strong hypotheses, and in no way claim to accurately represent reality. However, they are useful to (partly) answer the questions we asked in this thesis: can the structure of intraspecific variability arise from the structure of environmental variables that were not accounted for? Yes (Chapter 1). Does the way intraspecific variability is introduced in a community dynamics model matter for species coexistence and community composition? Yes (Chapter 2). Can the structure of intraspecific variability observed in data by Clark (2010) be explained simply by species responses to environmental variation? Yes (Chapter 3). Does this lead to coexistence? Yes, but this link must be discussed (Chapter 3 and General discussion). Can this structure of intraspecific variability alone reproduce patterns like species richness and diversity, species ranks or environmental filtering in a community dynamics model? Yes, but only partly (Chapter 3). By suggesting ways to improve the integration of the structure of intraspecific variability in community dynamics models, and particularly by proposing a method that allows species coexistence without fine-tuned parameters and can integrate field-data, we offer concrete perspectives for both fundamental and applied ecology.

VIII. Personal conclusion

Here I want to share more personal thoughts on my PhD experience.

This thesis finds itself in a scientific context that is not easy to grasp. Indeed, several schools of thought coexist (but compete!) to understand how species coexistence is possible. It did not take me long to understand that this was going to be one of the challenges of my PhD, and it was. It was difficult to navigate this heated scientific debate. I felt like I had to find a clear position, although it was difficult to feel legitimate to do so. For instance, there is this "neutrality *vs.* species differences" debate, where the definition itself of a species as well as its usefulness as a concept in ecology is disputed. I thought that old-school naturalists and botanists would be in the second team, as they have been describing precise species characteristics for centuries. I am attached to this aspect of biology. Therefore, I first felt like this was "the right way" for me, although I understood well how useful neutral theory was for ecology. I also felt like most ecologists I was working with strongly opposed neutral theory and wanted to show that species differences mattered. But later, thanks to other co-workers, I understood that it was not that contrasted. That the coexistence paradox could also be seen differently. For instance, we have many ways to explain coexistence, which ones are right? Or, isn't wanting to explain everything in a deterministic way (where what is not explained is considered as noise) a "physicist's" approach, far from the figure of the naturalist? I thus understood that I did not have to find a position, but to grasp how my work fitted in those different views.

Moreover, it was a challenge for me to feel adequate and useful in a working group such as INTRACO, with very talented and famous ecologists. However, the very friendly and supporting atmosphere of the group enabled me to make progress - although I am not there yet!

Finally, both points discussed above relate to finding one's place as a scientist. I think having spent a large part of my PhD under quarantine delayed my scientific and personal development. I understood what I had been missing when the lab came back to life: a stimulating working environment with casual scientific discussions, in-person seminars, *etc.* My favourite experiences in research are related to things we could not do under quarantine: a field-work mission, an international conference, discussing with people from the whole world who stay in the lab, going abroad for a workshop...I am grateful to still have experienced all this.

To conclude, like for most PhD student, this has been a difficult journey, but now that I look back I am proud of how far I have come.

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Appendices

Appendices of Chapter 1

Appendix 1: Simulation experiment with two species

Perfect knowledge model: generating response values.

We fixed the species parameters of the "Perfect knowledge model" as follows (see main text, Eq.1.1), using 10 environmental variables (N=10):

Parameters of species 1: $\beta_0 = 0.25$, $\beta_1 = 0.15$, β_2 to β_6 were chosen randomly between -0.05 and 0.05 and β_7 to β_{10} were chosen randomly between 0 and 0.05.

Parameters of species 2: $\beta_0 = 0.2$,, $\beta_1 = 0.1$, β_2 to β_{10} were chosen the same way as for species 1.

The difference between the species was imposed by those parameters. Here, species 1 was more competitive on average thanks to its higher intercept (β_0) and response to the first environmental variable (β_1) (see main text, Fig. 16). The first environmental variable (X_1) had a higher weight in the computation of the response variable, as would be the most limiting factor for the response variable.

To account for intrinsic variability in our generated data, we added variability in species parameters by sampling each individual parameter in a normal distribution centered on the species mean parameter and with a standard deviation of a quarter of the species mean parameter.

To represent the spatialized environment, we built a 2D matrix of dimension 500×500 for each environmental variable at a time t_0, by randomly generating them with spatial autocorrelation. Each variable was independently simulated by using the gstat R package (Pebesma 2004; Gräler et al. 2016), enabling to create autocorrelated random fields. A spherical semivariogram model was used for each of the ten environmental variables, with a mean of 0 for each explanatory variable (beta = 0), a sill of 1 (psill = 1) for each and a range of 50 (range = 50).

We then considered that Y had been measured at two times, t_0 and t_1, for each individual. A pair of coordinates within this spatialized environment was randomly assigned to each of the ‘r nind‘ individuals. We considered that some of the environmental variables (light, temperature, humidity, nutrient availability for instance) had changed between t_0 and t_1 and others had not (slope, altitude for instance). For the first environmental variable which had a stronger impact on Y values and another randomly drawn environmental variable, we computed values at t_1 as $t_0 + \epsilon$, $\epsilon \sim \mathcal{N}(0,1)$ (they randomly increased or decreased). For two other environmental variables randomly drawn, $X_{t_1} = X_{t_0} + |\epsilon|, \epsilon \sim \mathcal{N}(0,1)$ (they increase) and for two other environmental variables, $X_{t_1} = X_{t_0} - |\epsilon|, \epsilon \sim \mathcal{N}(0,1)$ (they decreased).

This led to two repeated measurements of Y for each individual of each species, *i.e.* 2,000 values of $Y_{i,j,t}$, with $i = [1;2]$; $j = [1,50]$; $t = [t_0;t_1]$.

Fig. 27 shows the distribution of the simulated Y data and Fig. 28 shows the relationship between X_1 and Y.

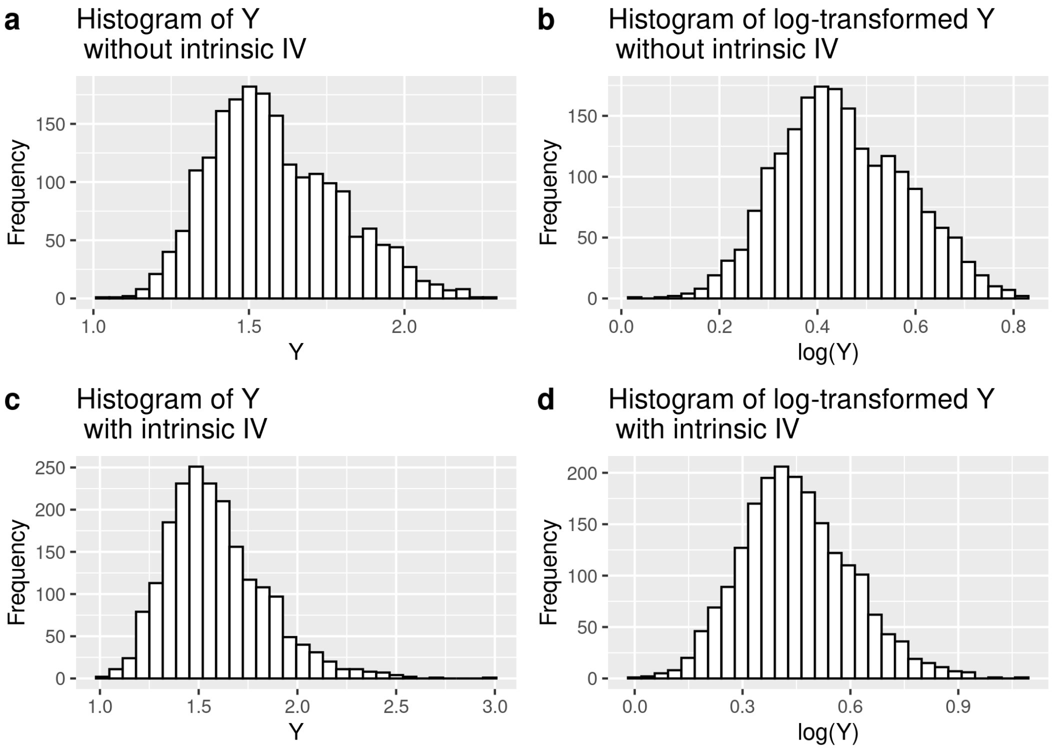


Figure 27: Histograms of the simulated Y values (a) without intrinsic IV **(b)** without intrinsic IV and log-transformed **(c)** with intrinsic IV **(d)** with intrinsic IV and log-transformed.

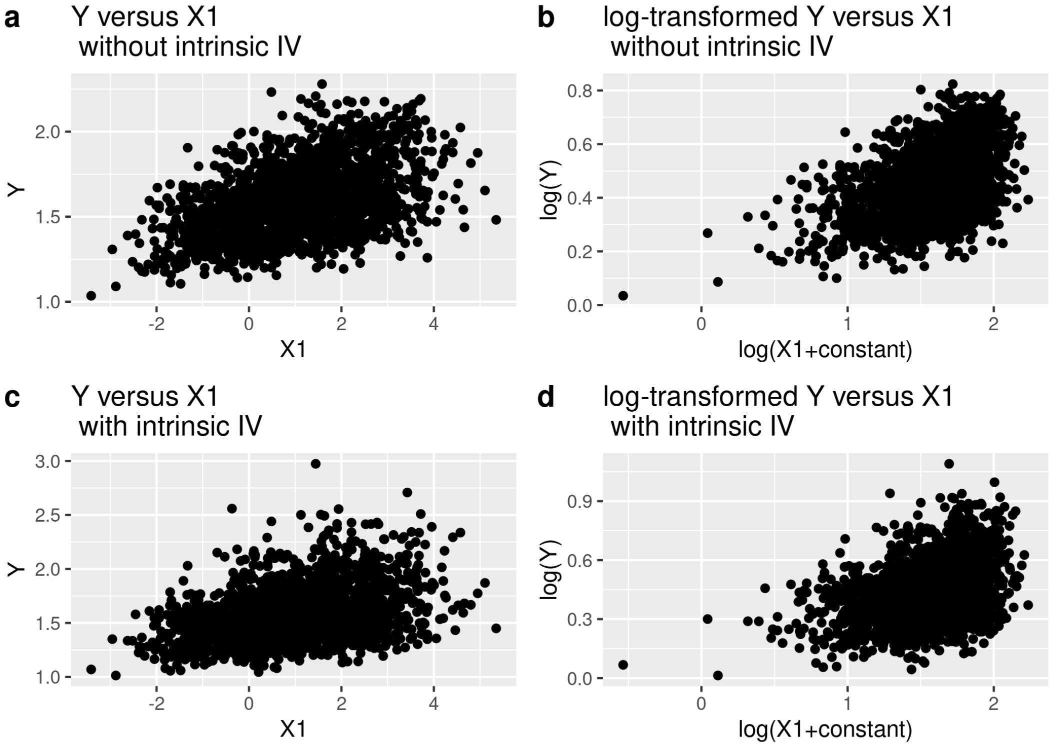


Figure 28: Histograms of the simulated Y values (a) without intrinsic IV **(b)** without intrinsic IV and log-transformed **(c)** with intrinsic IV **(d)** with intrinsic IV and log-transformed.

Imperfect knowledge model: interpreting the response values with only one explanatory variable.

We ran the model (see main text, Eq.1.2) twice, with the datasets generated with and without intrinsic IV. We visualized the convergence and the results of the models thanks to trace and density plots.

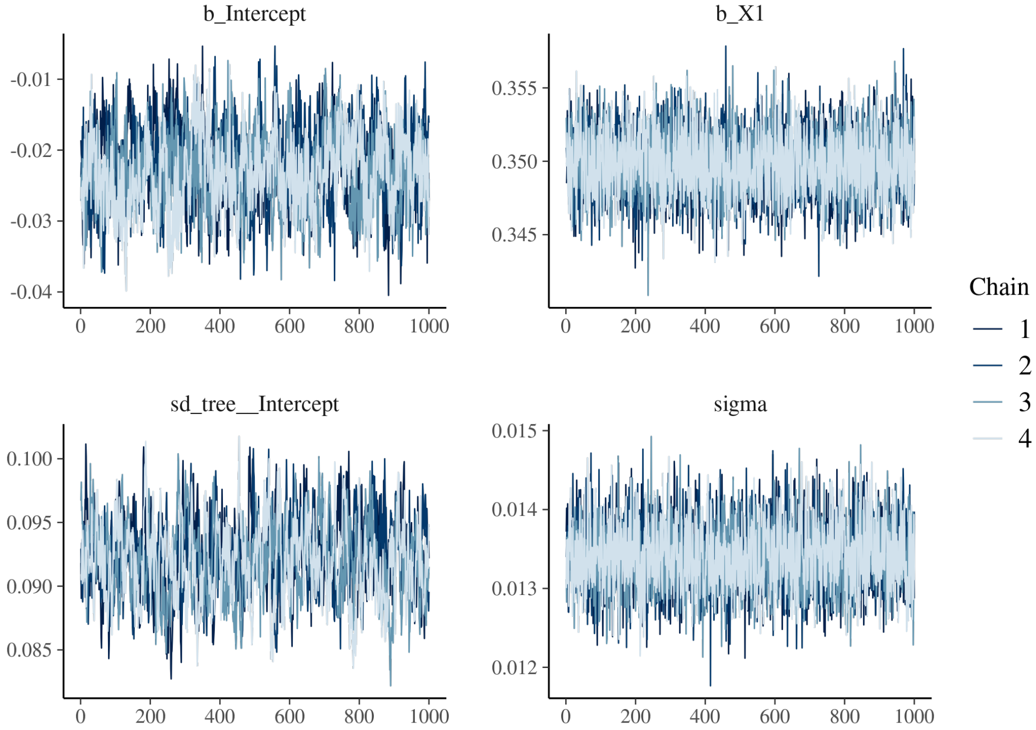


Figure 29: Trace of the posterior of the model for Species 1 without intrinsic IV

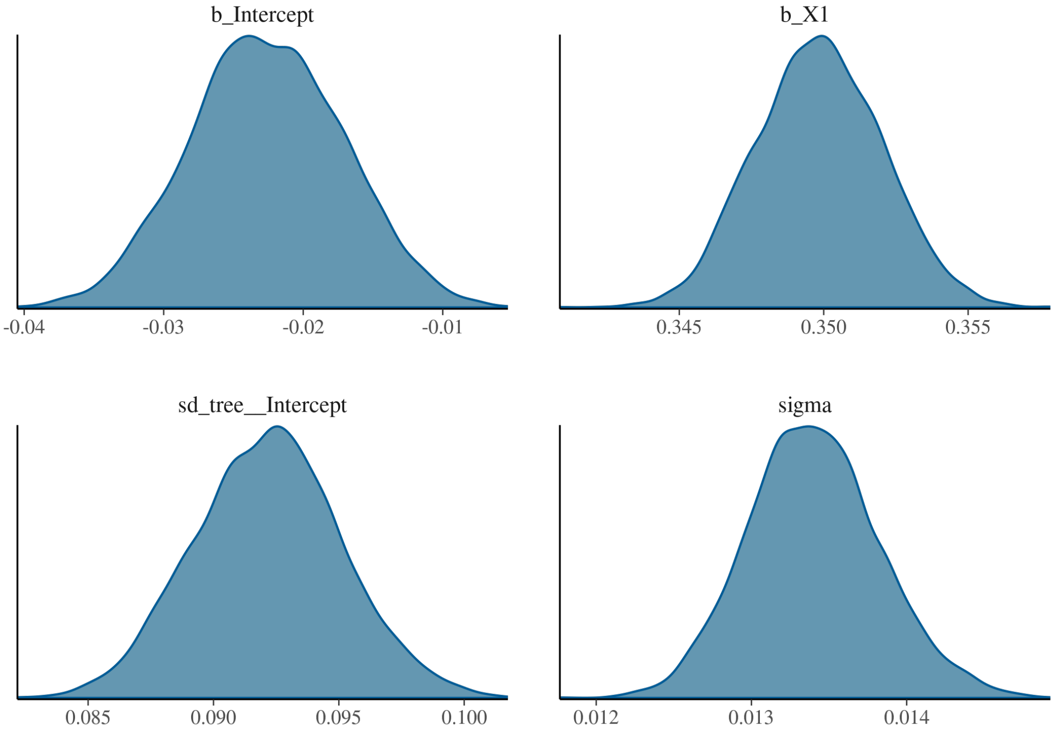


Figure 30: Density of the posterior of the model for Species 1 without intrinsic IV

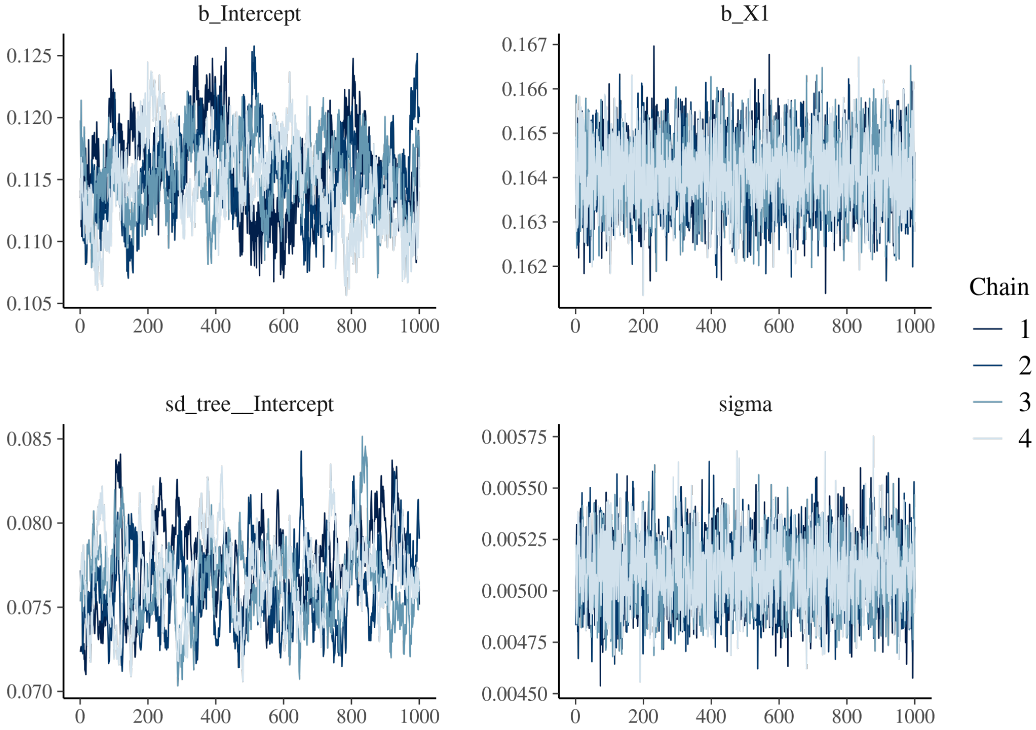


Figure 31: Trace of the posterior of the model for Species 2 without intrinsic IV

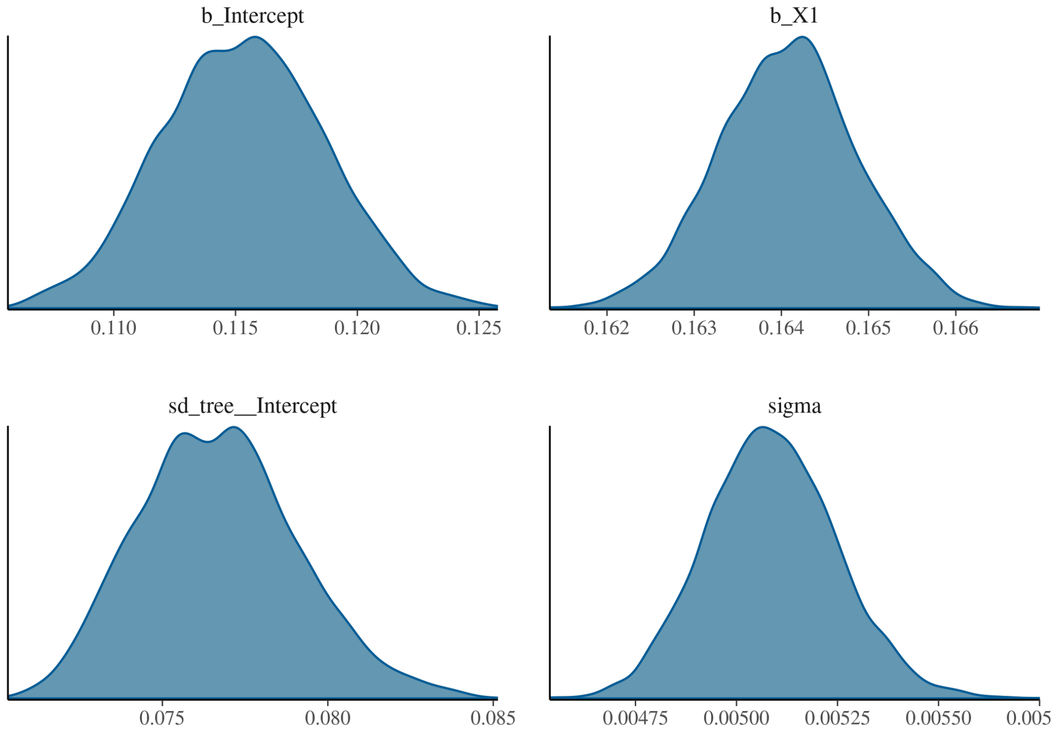


Figure 32: Density of the posterior of the model for Species 2 without intrinsic IV

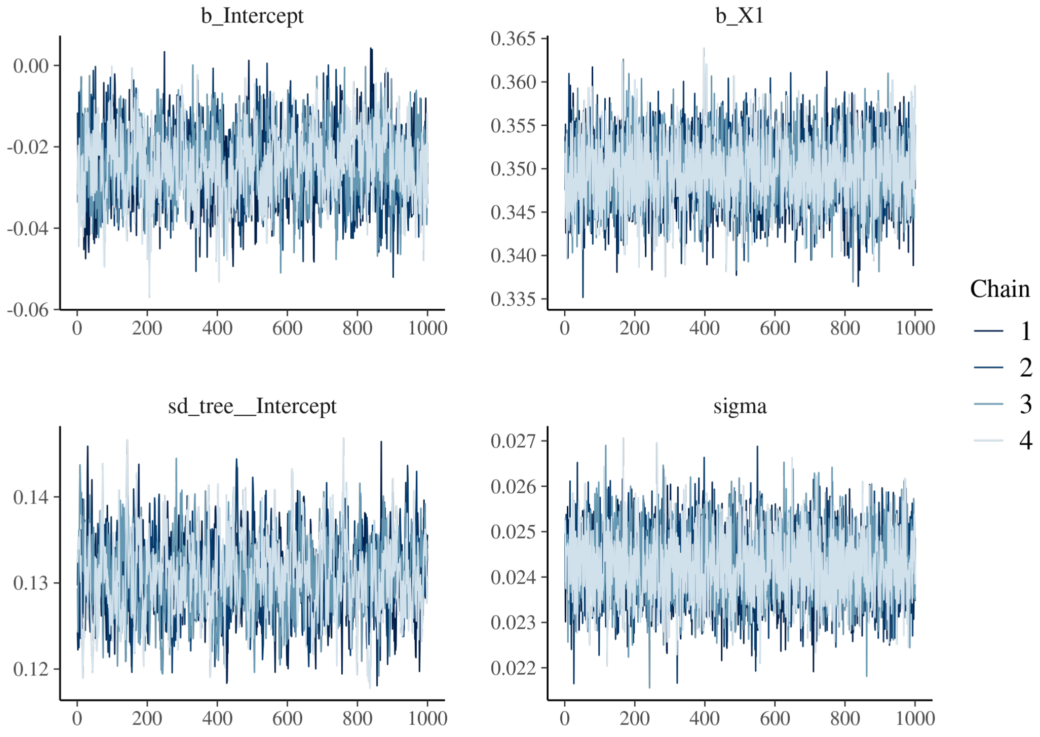


Figure 33: Trace of the posterior of the model for Species 1 with intrinsic IV

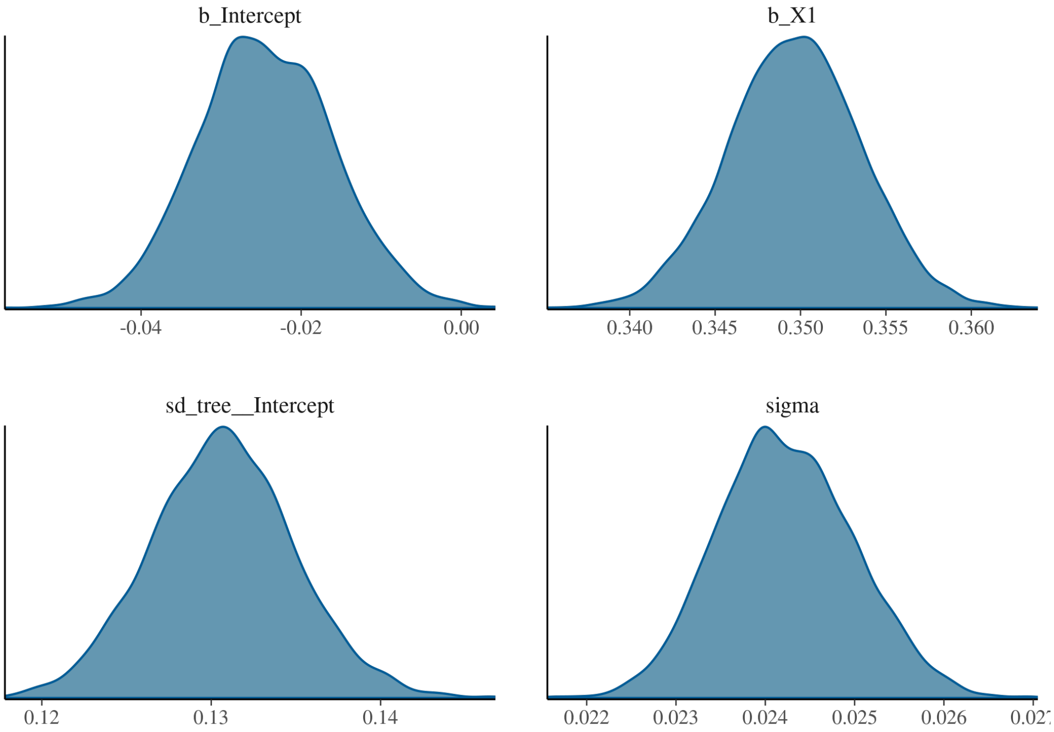


Figure 34: Density of the posterior of the model for Species 1 with intrinsic IV

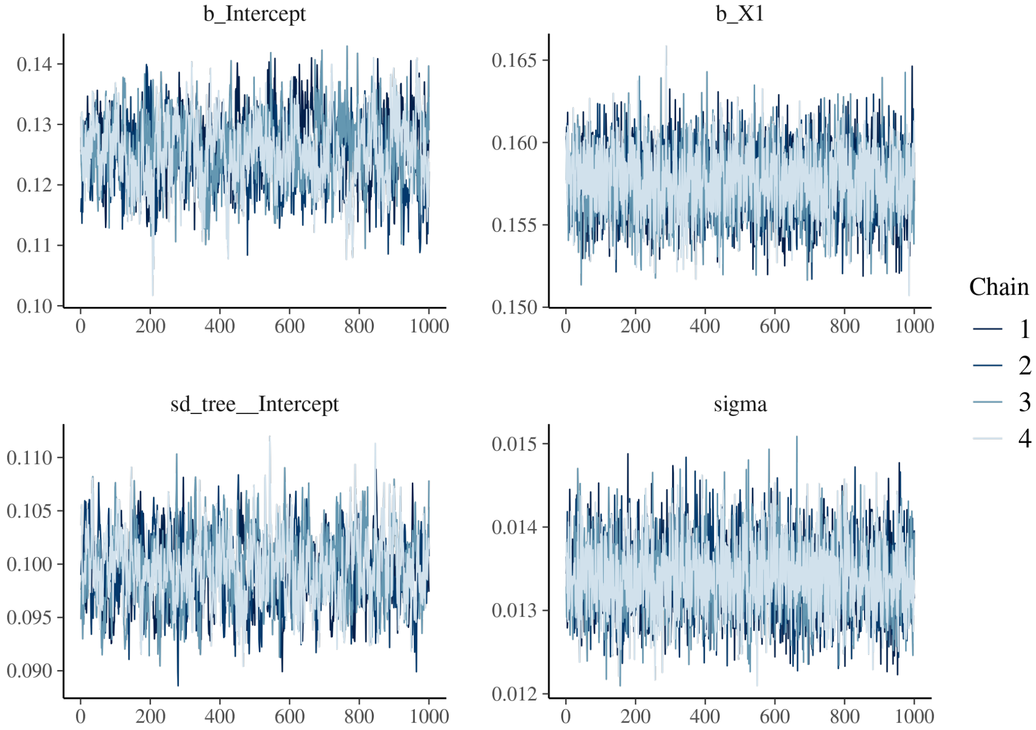


Figure 35: Trace of the posteriors of the model for Species 2 with intrinsic IV

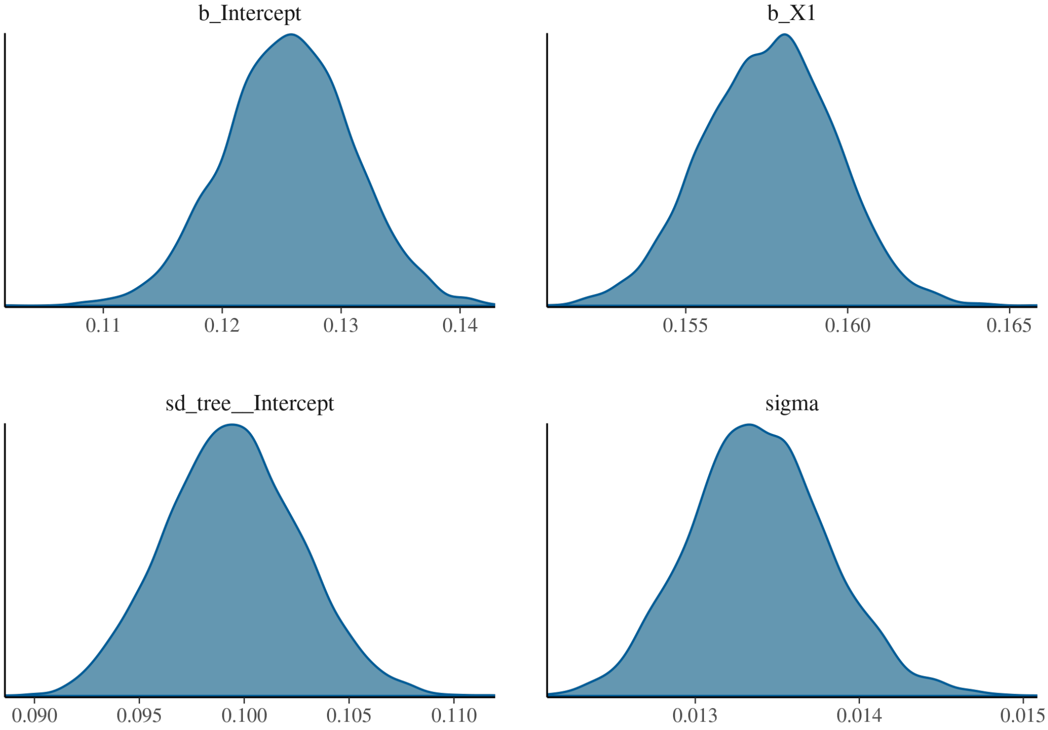


Figure 36: Density of the posteriors of the model for Species 2 with intrinsic IV

Models converged and we inferred a high IV even in the absence of intrinsic IV (Table 9).

Table 9: Summary of the model's outputs

	β_0	β_1	V_b	V)
Species 1 (no random IV)				
Estimate	-2.3e-02	3.5e-01	9.2e-02	1.3e-02
Estimation error	5.5e-03	2.2e-03	2.9e-03	4.2e-04
95% interval	-3.3e-02 - -1.2e-02	3.5e-01 - 3.5e-01	8.7e-02 - 9.8e-02	1.3e-02 - 1.4e-02
R-hat	1e+00	1e+00	1e+00	1e+00
Bulk ESS	3.6e+02	4.3e+03	4.7e+02	3.7e+03
Tail ESS	1.1e+03	3.9e+03	7.5e+02	3.8e+03
Species 2 (no random IV)				
Estimate	1.2e-01	1.6e-01	7.7e-02	5.1e-03
Estimation error	3.3e-03	8e-04	2.4e-03	1.6e-04
95% interval	1.1e-01 - 1.2e-01	1.6e-01 - 1.7e-01	7.2e-02 - 8.2e-02	4.8e-03 - 5.4e-03
R-hat	1e+00	1e+00	1e+00	1e+00
Bulk ESS	6.5e+01	4e+03	1.3e+02	3.6e+03
Tail ESS	1.8e+02	4e+03	3.8e+02	3.8e+03
Species 1 (with random IV)				
Estimate	-2.4e-02	3.5e-01	1.3e-01	2.4e-02
Estimation error	8.4e-03	3.9e-03	4.2e-03	7.6e-04
95% interval	-4.1e-02 - -7.8e-03	3.4e-01 - 3.6e-01	1.2e-01 - 1.4e-01	2.3e-02 - 2.6e-02
R-hat	1e+00	1e+00	1e+00	1e+00
Bulk ESS	8.5e+02	4e+03	8.7e+02	4.1e+03
Tail ESS	2.1e+03	4e+03	1.5e+03	3.8e+03
Species 2 (with random IV)				
Estimate	1.3e-01	1.6e-01	9.9e-02	1.3e-02
Estimation error	5.4e-03	2e-03	3.2e-03	4.2e-04
95% interval	-4.1e-02 - 1.4e-01	1.5e-01 - 1.6e-01	9.3e-02 - 1.1e-01	1.3e-02 - 1.4e-02
R-hat	1e+00	1e+00	1e+00	1e+00
Bulk ESS	3.5e+02	4e+03	6.3e+02	3.9e+03
Tail ESS	1e+03	4e+03	1.4e+03	3.9e+03

Table 10: Results of the Morans's I test for both species separatly and together.

	Moran's I	P-value
Species 1	5.3e-02	0e+00
Species 2	5e-02	0e+00
All individuals	3.4e-02	0e+00

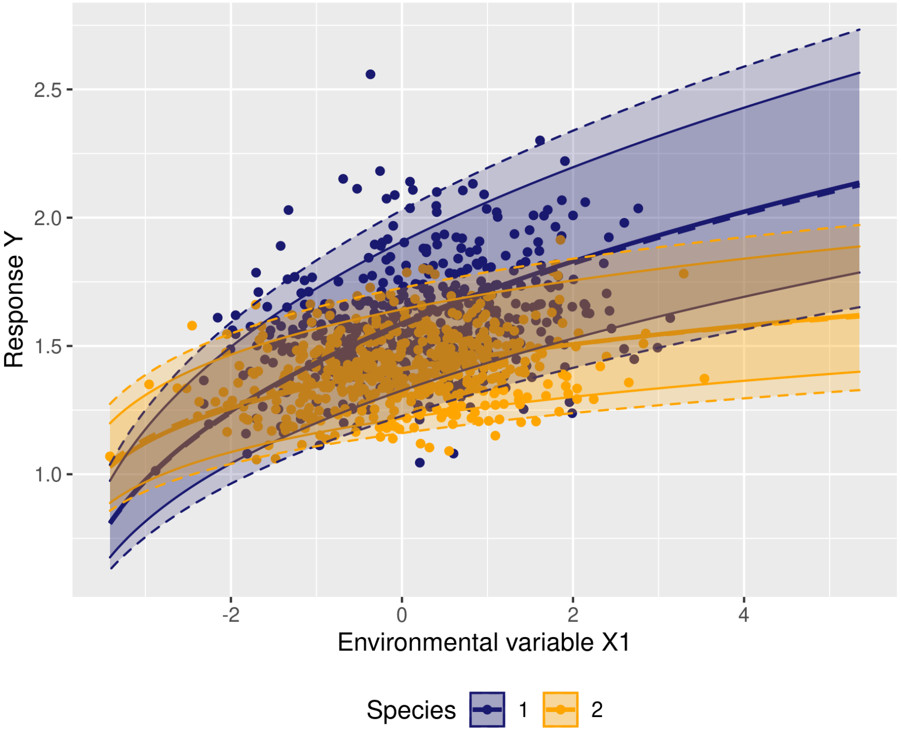


Figure 37: Plot of the real values - points - and estimated mean - bold lines - and 95% confidence interval - thin lines - of Y versus X_1. The dashed lines correspond to the 95% interval due to intrinsic IV.

In Fig. 37 the bold and solid (dashed) lines represent the mean rate of the response variable (*e.g.* growth) of Species 1 (blue) and Species 2 (orange) as computed with the parameters retrieved from the model without (with) intrinsic IV respectively. The plain lines represent the 95% interval of the posteriors from the model without intrinsic IV and the dashed lines show the 95% confidence interval of the posteriors from the model with intrinsic IV. Fig. 37 shows that intrinsic IV simply increases the overlap between the response of Species 1 and Species 2.

Spatial autocorrelation of individual response

To test for spatial autocorrelation of individual response, we computed Moran's I test using the Moran.I function of the ape R package (Paradis and Schliep 2019).

Similarity between conspecific individuals compared to heterospecific individuals and consequences for species coexistence.

We used semivariograms to visualise the spatial autocorrelation of the response variable and to test whether the individual response was more similar within conspecifics than within heterospecifics. The semivariograms were computed and modelled with the variogram and the fit.variogram functions of the gstat R package (Pebesma 2004; Gräler et al. 2016) respectively. The variogram models were spherical.

Appendix 2: Analysis of an Eucalyptus clonal plantation dataset

Data and preliminary analysis

The experimental design aimed at minimizing environmental variations and selected productive genotypes able to accommodate several environmental conditions (le Maire et al. 2019).

Mean annual growth of each tree in mm yr^{-1} was computed as the DBH (Diameter at Breast Height) difference between two consecutive censuses divided by the time between the two censuses. In case of mortality of the tree between two censuses, the data was discarded. We computed the neperian logarithm of diameter and growth (with a constant for growth in order to avoid undefined values).

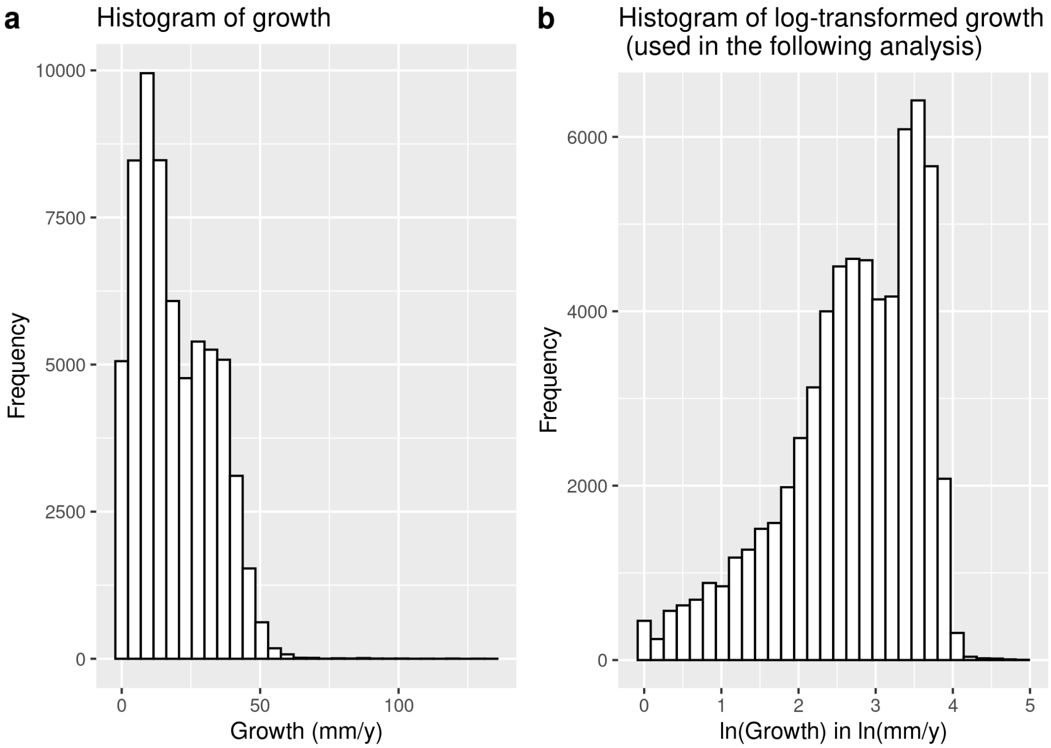


Figure 38: Growth (after removing data after mortality) before (a) and after (b) log-transformation.

Fig. 38 shows the distribution of growth data before and after log-transformation.

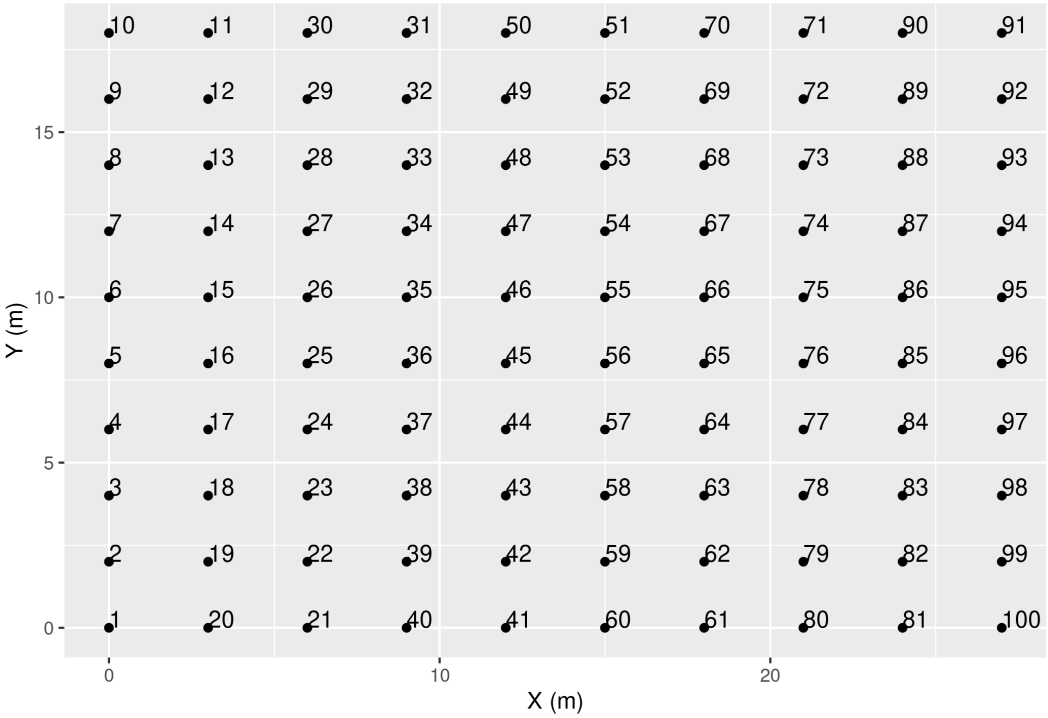


Figure 39: Design of a plot. Each point is a tree and the associated number is the tag of the tree.

Fig. 39 shows the disposition of the trees in a single plot. There are 14 genotypes times 10 repetitions, so 140 plots with this same design.

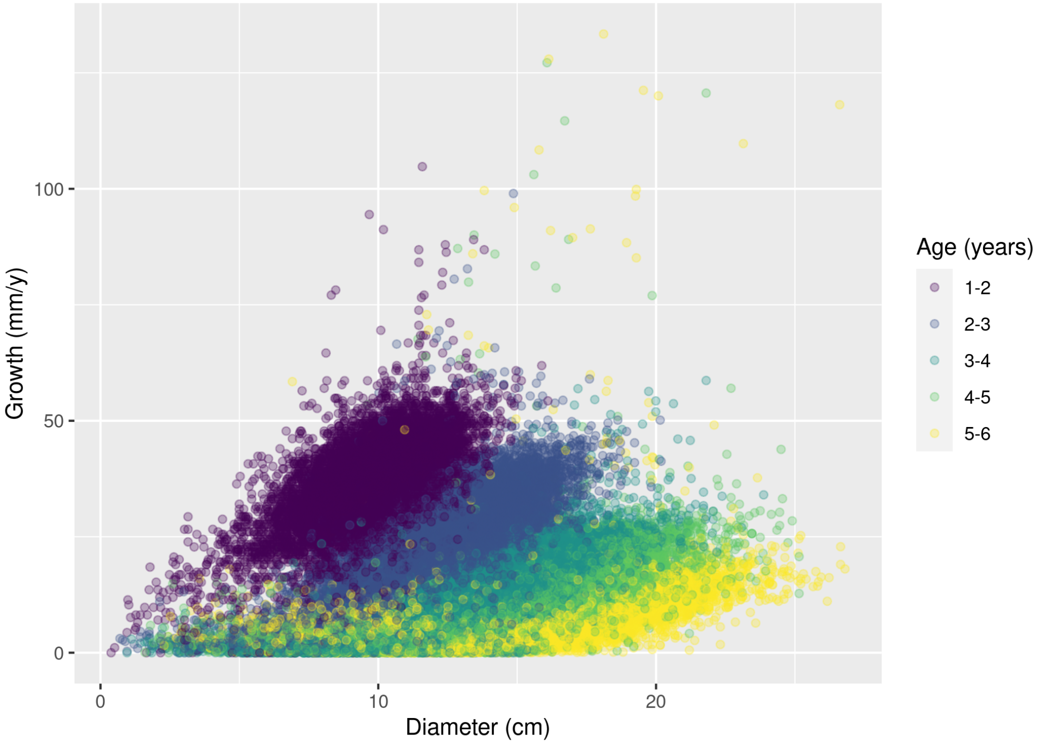


Figure 40: Plot of the growth versus the diameter. Each colour represents a tree age.

Fig. 40 shows the age of the trees has a big influence on the values of growth but also on the relationship between growth and diameter: the slope is smaller with time, indicating that for the same diameter, growth is slower through time. This is likely an effect of competition for light and possibly underground resources, since as the trees grow their capacity to capture resources increases. Therefore, we computed a competition index $C_{i,t}$ to integrate this effect in the growth model. The competition index was computed for each tree which is not on the edge of a plot. It was the sum of the basal areas (BA) of the 8 direct neighbours (there was no need to divide by the area of the rectangle that comprises all the direct neighbours, since this latter is a constant by construction of the experimental design). It was then log-transformed. Dead neighbours were considered as having a null BA.

$$C_{i,t} = \sum BA_{neighbours(i,t)}$$

Estimation of intraspecific variability

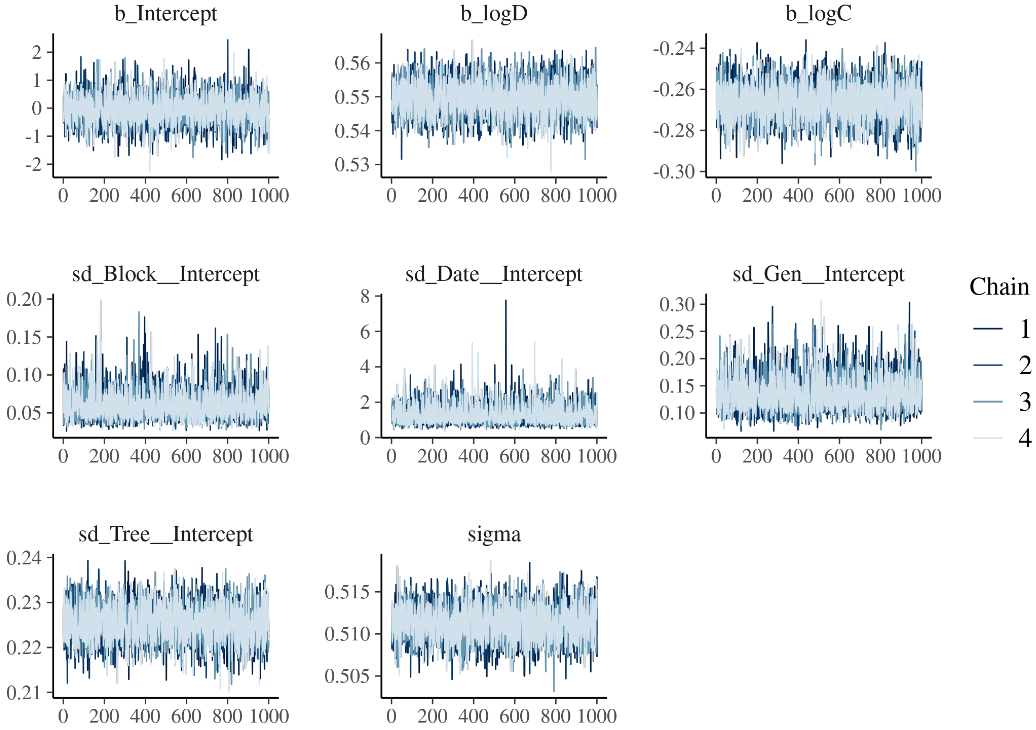


Figure 41: Trace of the posteriors of the inferred parameters.

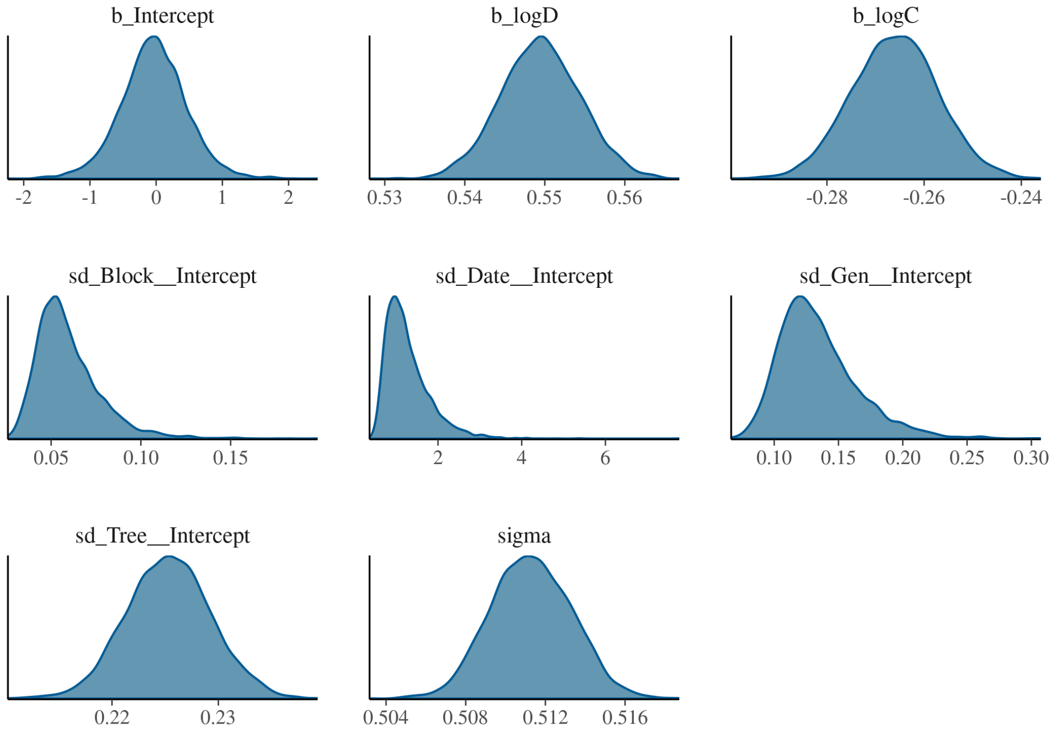


Figure 42: Density of the posteriors of the inferred parameters.

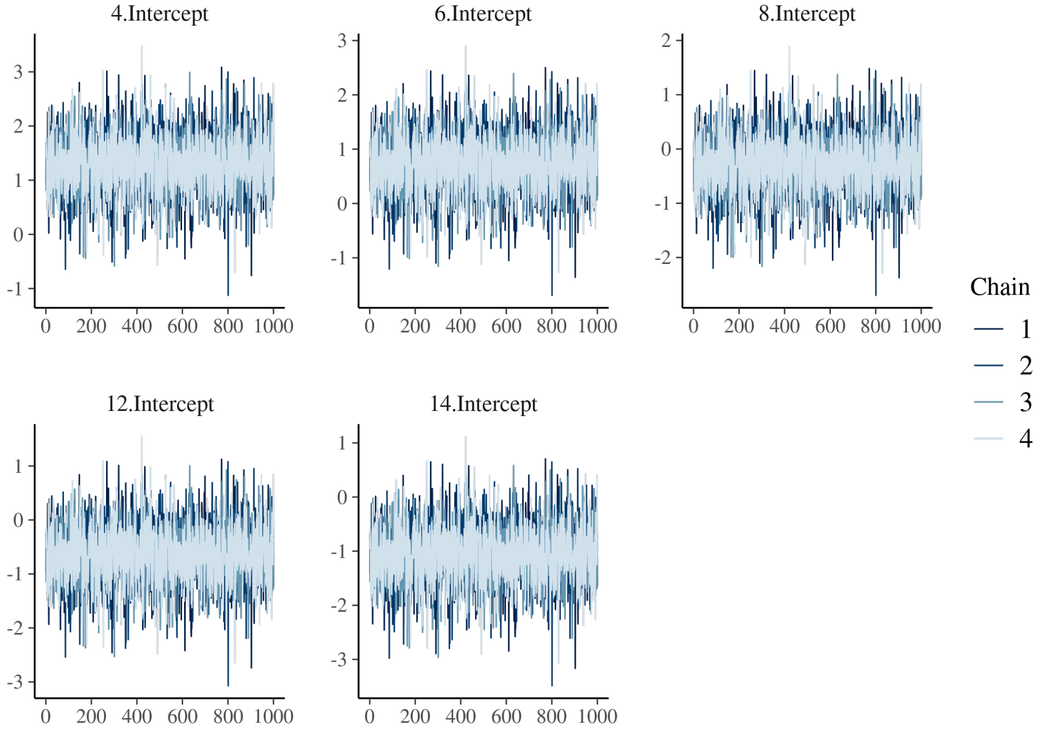


Figure 43: Trace of the temporal random effects.

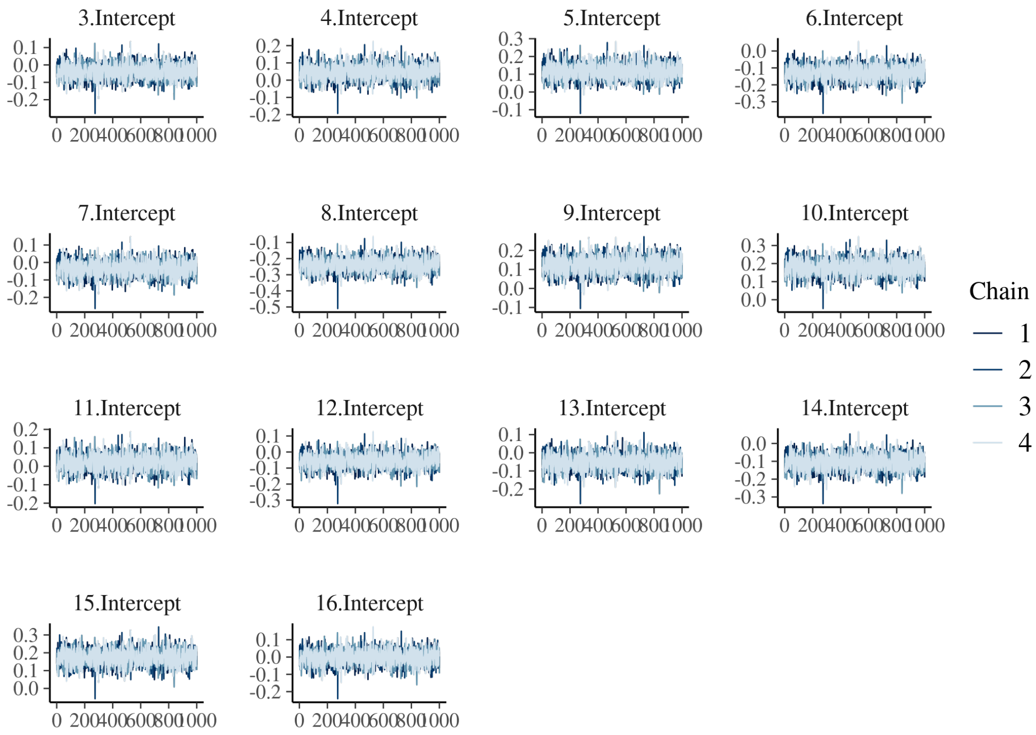


Figure 44: Trace of the genotype random effects.

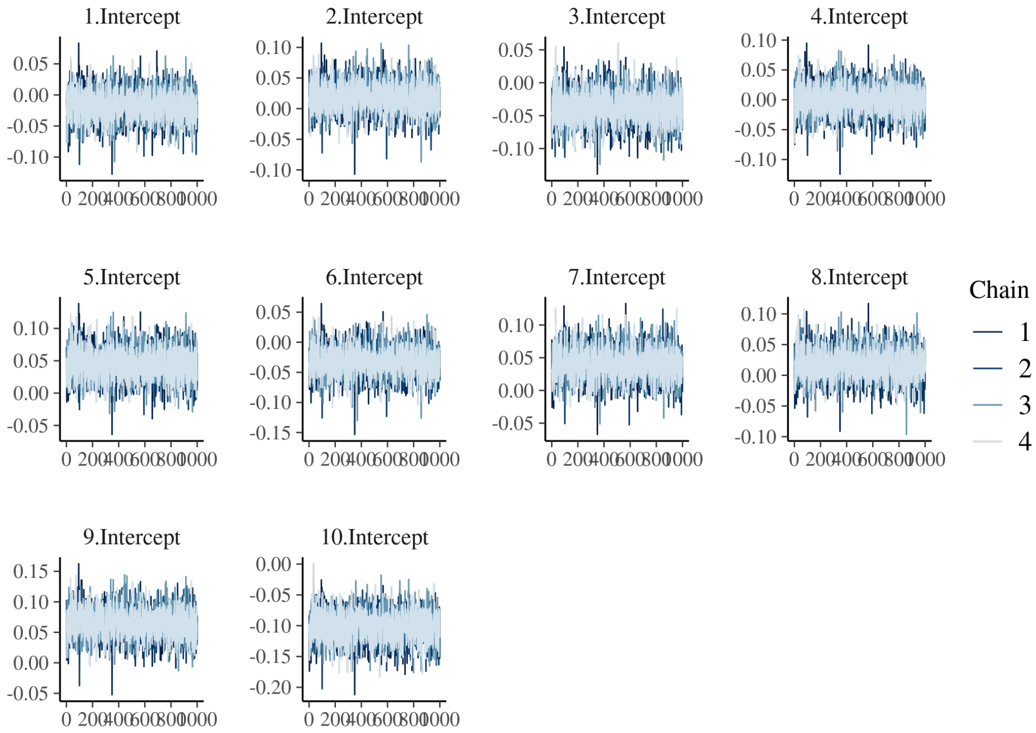


Figure 45: Trace of the spatial (block) random effects.

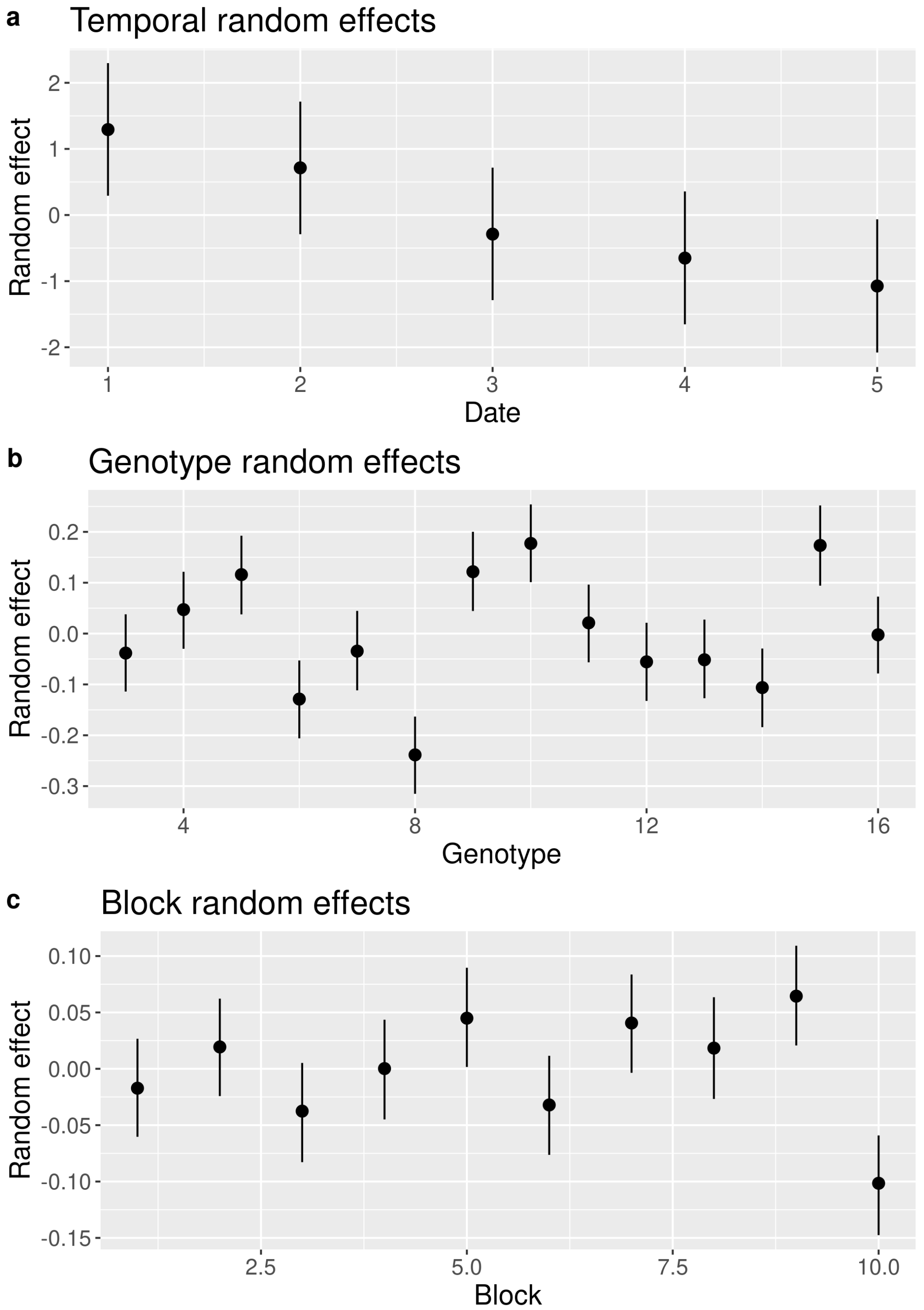


Figure 46: Mean values and 95% confidence interval of the temporal, genetic and spatial and random effects.

Fig. 41 to 45 illustrate the convergence of the model. Fig. 46 shows mean values and 95% confidence intervals of random effects (except individual random effects which are too many), enabling to graphically look for a tendency. Table 11 displays details on model convergence and reliability.

Table 11: Summary of the model's outputs

	Intercept (β_0)	**Diameter** (β_1)	**Competition** (β_2)	**Individual variance** (V_i)	**Block variance** (V_b)	**Genetic variance** (V_g)	**Temporal variance** (V_t)	**Residual variance** (V)
Estimate	-3.50e-02	5.50e-01	-2.70e-01	2.30e-01	6.00e-02	1.30e-01	1.30e+00	5.10e-01
Estimation error	5.00e-01	5.00e-03	8.90e-03	4.00e-03	1.80e-02	3.10e-02	5.40e-01	2.00e-03
95% interval	-1e+00 - 9.8e-01	5.4e-01 - 5.6e-01	-2.8e-01 - - 2.5e-01	2.2e-01 - 2.3e-01	3.5e-02 - 1e-01	8.9e-02 - 2.1e-01	6.2e-01 - 2.6e+00	5.1e-01 - 5.2e-01
R-hat	1e+00	1e+00	1e+00	1e+00	1e+00	1e+00	1e+00	1e+00
Bulk ESS	3.3e+03	3.8e+03	3.8e+03	3.6e+03	3.3e+03	3.1e+03	3.4e+03	3.9e+03
Tail ESS	3.7e+03	3.9e+03	3.6e+03	3.5e+03	3.6e+03	3.7e+03	3.6e+03	3.8e+03

Appendix 3: Analysis of tropical forest inventory data

Datasets

Paracou The Paracou forest is located in French Guiana. It is one of the best-studied lowland tropical forests in the Guiana Shield region. It belongs to the Caesalpiniaceae facies and has amongst the highest alpha-diversity in the Guiana shield with 150-200 tree species per hectare in inventories of trees with DBH $\geq$ 10 cm. The Guiana Shield is characterized by Pre-Cambrian granitic and metamorphic geological formations, highly eroded. It is associated with gently undulating landscapes and a very dense hydrographic system. Paracou forest lies in a hilly area, on a formation called "série Armina" characterized by schists and sandstones and locally crossed by veins of pegmatite, aplite and quartz. The topography of the site consists of small hills separated by narrow ($<$ 5 m wide) sandy waterbeds. The altitude varies from 5 to about 45 m above sea level Gourlet-Fleury et al. 2004; Hérault and Piponiot 2018. The mean annual temperature is 26 °C and winds are generally weak. There is a well marked dry season (from mid-August to mid-November) and a long rain season with a short drier period between March and April (mean annual rainfall of 3,041 mm). Different study programs have been led at the Paracou site (`https://paracou.cirad.fr/`). Here, we used data from a disturbance experiment, where 12 square plots of 6.25 ha were exposed to four different logging intensities between 1986 and 1988, as well as four square plots of 6.25 ha which were set up for biodiversity monitoring in 1990-1992 (plots 1-15). Since then, cartesian coordinates, DBH, species identity and survival of each tree with a DBH $\geq$ 10 cm have been collected every one or two years, during the dry season (mid-August to mid-November). The studied 93.75-ha area harbors 91284 measured trees, among which 21688 belong to an undetermined species and others belong to 614 determined species, 221 genera and 64 families.

We removed all measures of the years before the perturbations were performed and the biodiversity plots were added (1985-1991), thus obtaining a dataset containing 91029 measured trees, among which 21481 belong to an undetermined species and others belong to 614 determined species, 221 genera and 64 families.

Fig. 47 shows the location of the used trees in the Paracou site.

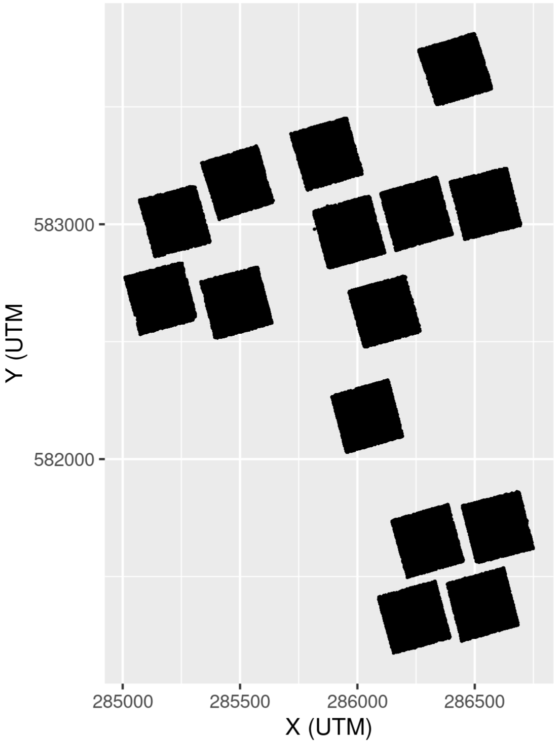


Figure 47: Plots at the Paracou site. Each point is a tree.

Uppangala The Uppangala Permanent Sample Plot (UPSP) is located in South-East Asia, in the Western Ghats of India, and was established in 1989 by the French Institute of Pondicherry in the Kadamakal Reserve Forest, in the Pushpagiri Wildlife Sanctuary, in Karnataka state, India Pélissier et al. 2011. It is a low altitude (500-600 m) wet evergreen monsoon Dipterocarp forest Le Bec et al. 2015. This forest is considered as one of the rare undisturbed tropical forests in the world Pascal and Pelissier 1996. The studied area of 5.07 ha is quite steep, with a mean slope angle of about 30–35°. The plots consist in five North–South oriented transects that are 20-m wide, 180- to 370-m long, and 100-m apart center to center, in addition to three rectangular plots which overlap the transects. The transects gather data from 1990 to 2011 and the rectangular plots from 1993 to 2011. The trees with GBH (Girth at Breast Height) $\geq$ 30 cm (equivalent to ca. 9.5 cm DBH) were measured every 3 to 5 years. The original dataset contains measurements of 3870 trees of 102 species (including 2 morphospecies),78 genera and 32 families.

We removed the census dates which were not common for all plots (1990-1992).

Thus, we obtained a dataset containing 3870 trees of 102 species (including 2 morphospecies),78 genera and 32 families.

Fig. 48 shows the location of the trees in the Uppangala site.

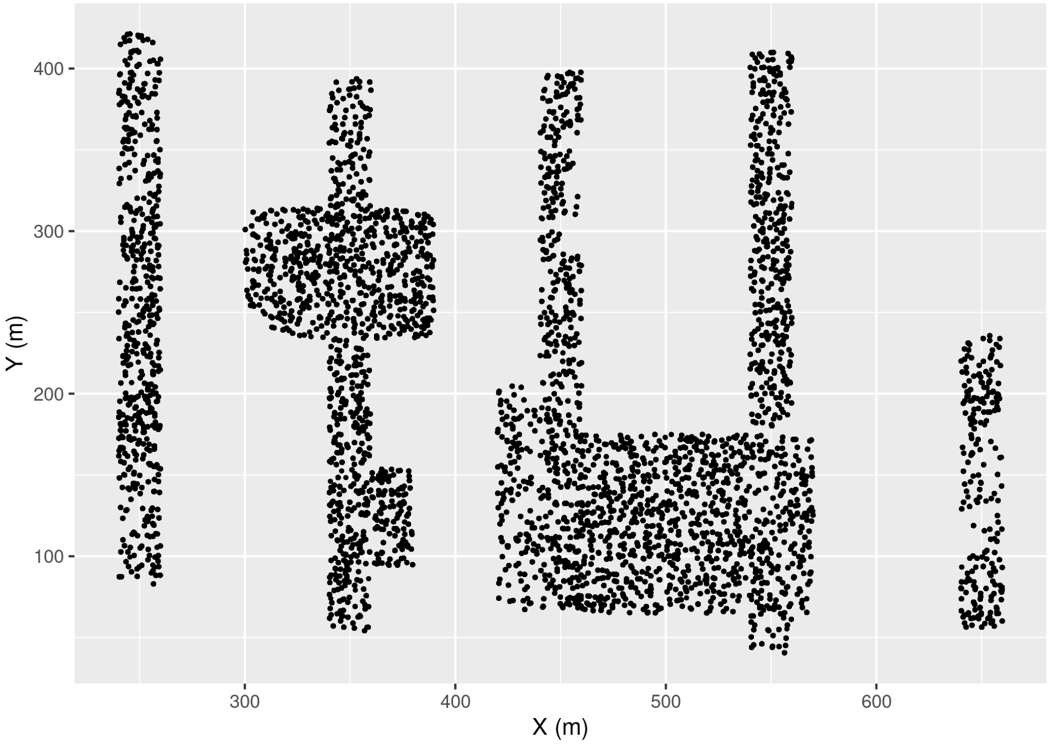


Figure 48: Plots at Uppangala site. Each point is a tree.

BCI The Barro Colorado Island site is located in central America, in Panama, covered by a lowland tropical moist forest. The zone became an island after a valley was flooded in order to build the Panama Canal, in 1913. It is nowadays considered as the most intensively studied tropical forest in the world. The studied site is a 50 ha plot (500 × 1,000 m). It has an elevation of 120 m and is quite flat (most slopes are gentler than 10°). Complete censuses of all trees with DBH $\geq$ 1 cm have been performed every 5 years since 1980.

The dataset contains measurements of 423617 trees of 328 tree species, 195 genera and 63 families.

When only taking into account trees with DBH 10 cm for consistency with the other datasets, it contains measurements of 37224 trees of 255 tree species, 167 genera and 59 families. The dataset is available in (Condit et al. 2019).

Fig. 49 shows the location of the selected trees in the BCI site.

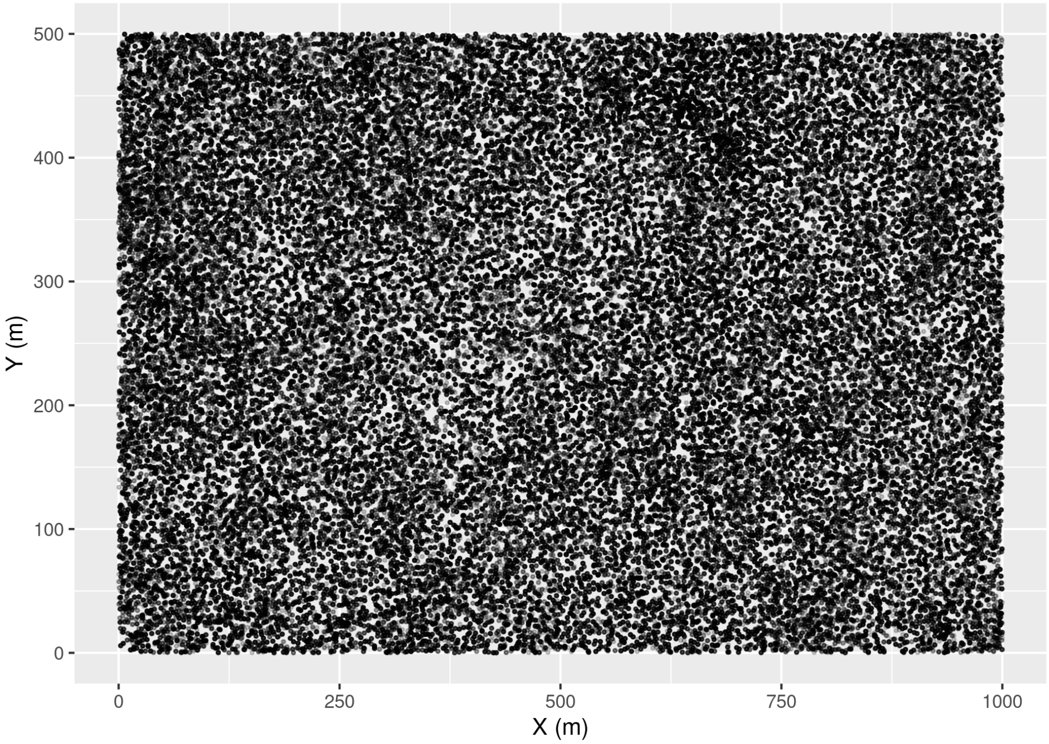


Figure 49: The 50 ha plot of the Barro Colorado Island site. Each point is a tree.

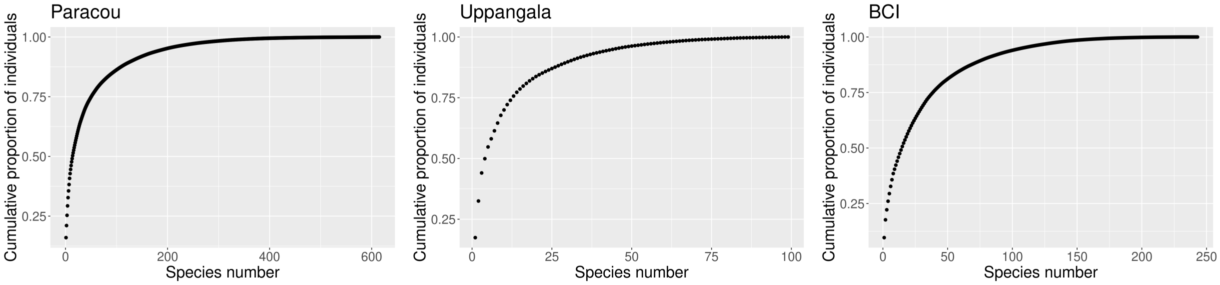


Figure 50: Abundance diagrams for the three study sites. For the Paracou site, only individuals that were identified to the species level are accounted for. The three communities include few dominant species and many rare species (long asymptote).

Growth and mean growth estimation

For the Paracou site, after removing 105836 growth estimates for 12520 trees of indeterminate species, we obtained a dataset with 931389 growth estimates for 65769 trees of 614 species.

For the Uppangala site, we obtained a dataset with 57921 growth estimates for 3725 trees of 102 species.

For the BCI site, we obtained a dataset with 167618 growth estimates for 30386 trees of 244 species.

Estimation of IV

We evaluated the convergence of the model using trace and density plots of the posterior estimates.

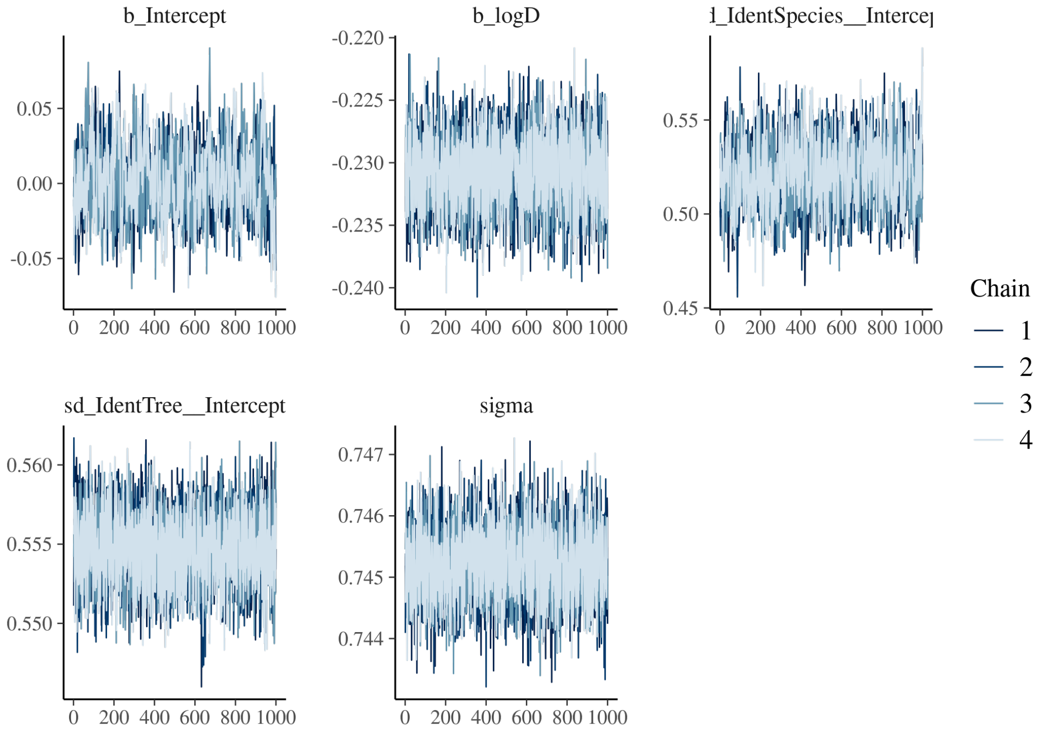


Figure 51: Trace of the posterior estimates for the Paracou site.

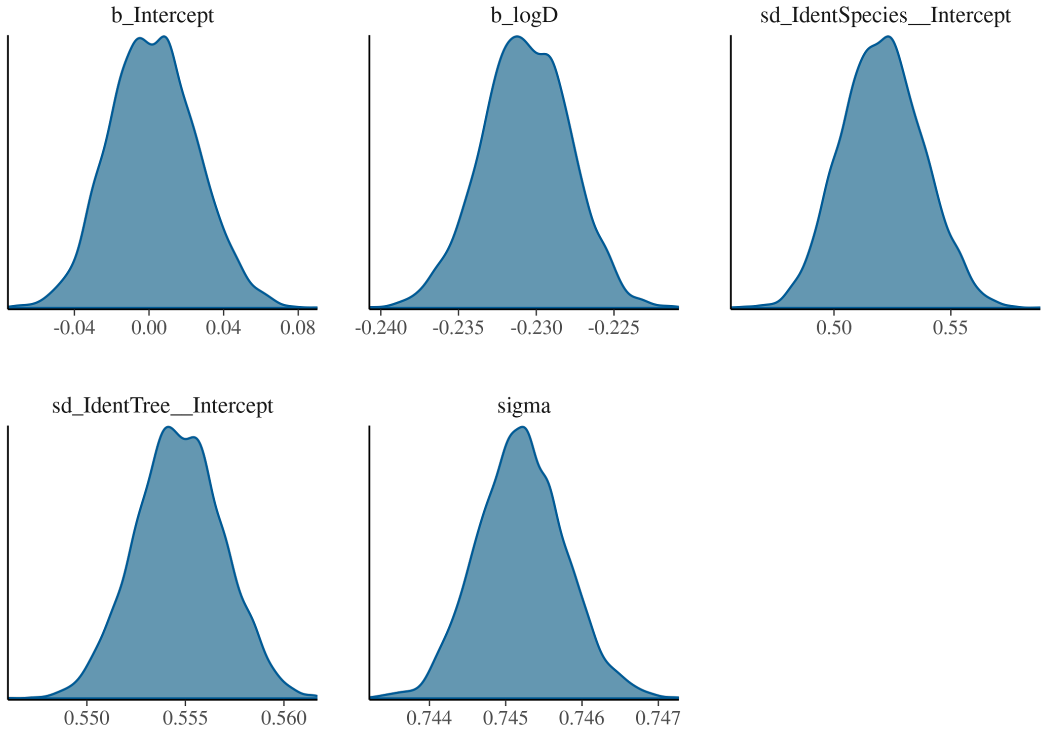


Figure 52: Density of the posterior estimates for the Paracou site.

Paracou

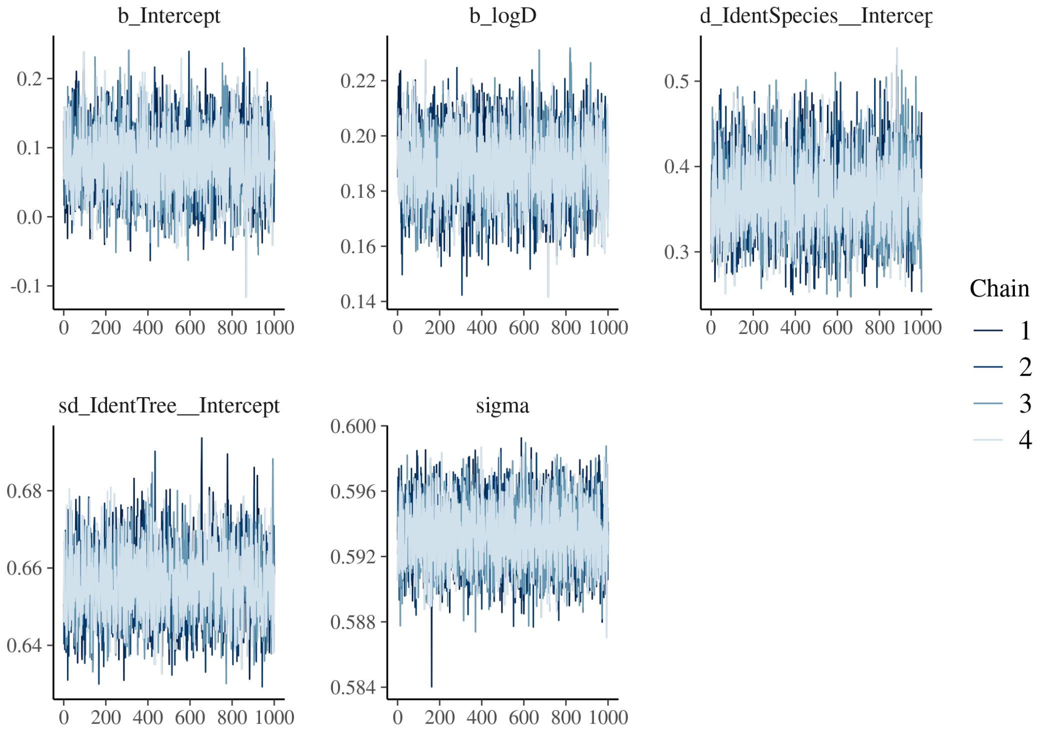


Figure 53: Trace of the posterior estimates for the Uppangala site.

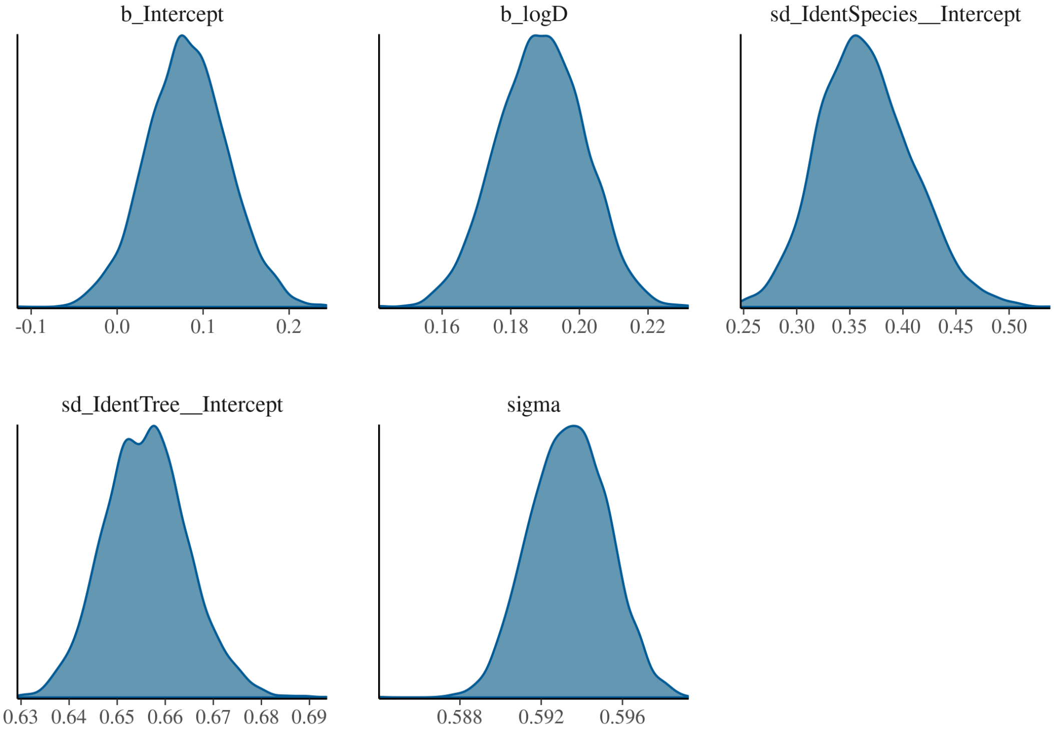


Figure 54: Density of the posterior estimates for the Uppangala site.

Uppangala

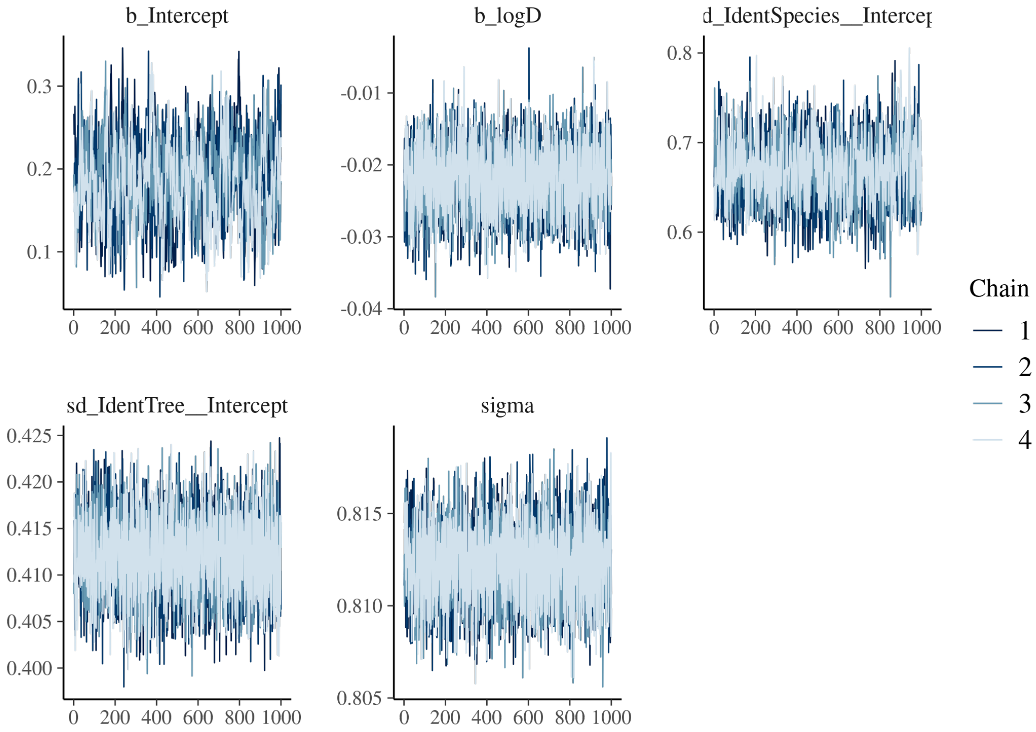


Figure 55: Trace of the posterior estimates for the BCI site.

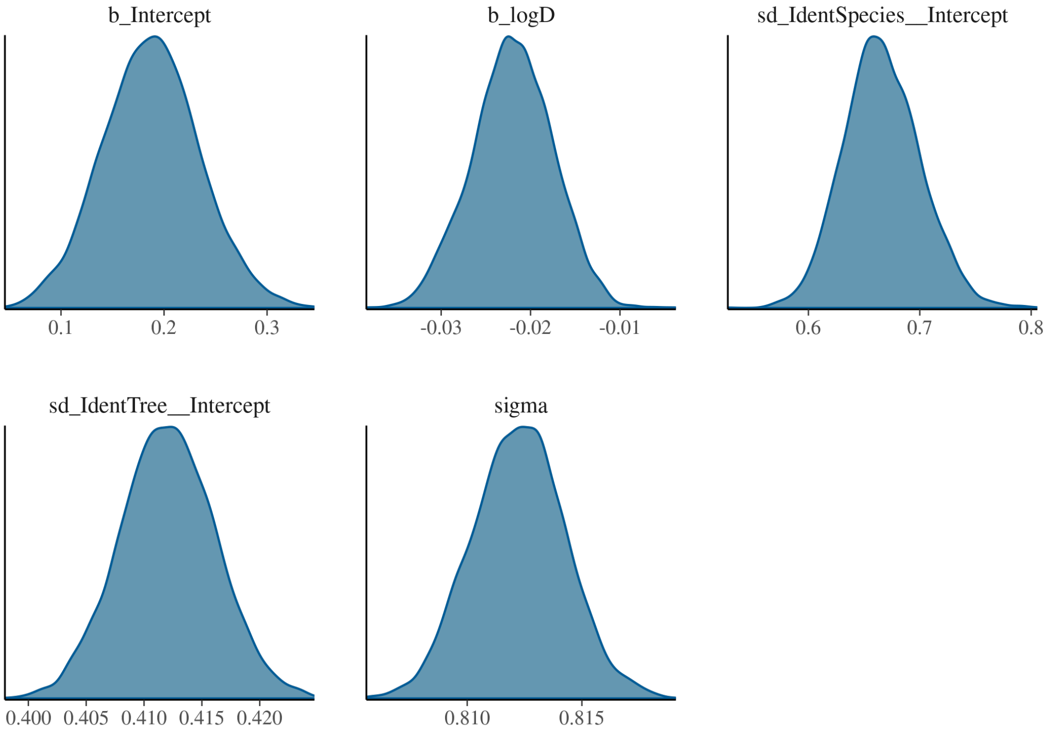


Figure 56: Density of the posterior estimates for the BCI site.

BCI

Table 12: Summary of the model's outputs

	Intercept (β_0)	**Diameter** (β_1)	**Species variance** (V_{bj})	**Individual variance** (V_{bi})	**Residual variance** (V)
Paracou					
Estimate	2.30e-03	-2.30e-01	5.20e-01	5.50e-01	7.50e-01
Estimation error	2.30e-02	2.80e-03	1.70e-02	2.20e-03	5.70e-04
95% interval	-4.1e-02 - 4.8e-02	-2.4e-01 - -2.3e-01	4.9e-01 - 5.6e-01	5.5e-01 - 5.6e-01	7.4e-01 - 7.5e-01
R-hat	1e+00	1e+00	1e+00	1e+00	1e+00
Bulk ESS	5.4e+02	2.5e+03	9.2e+02	2.6e+03	3.8e+03
Tail ESS	9e+02	3.2e+03	1.9e+03	3.1e+03	3.8e+03
Uppangala					
Estimate	8.20e-02	1.90e-01	3.70e-01	6.60e-01	5.90e-01
Estimation error	4.70e-02	1.30e-02	4.40e-02	8.60e-03	1.90e-03
95% interval	-1.1e-02 - 1.8e-01	1.6e-01 - 2.1e-01	2.8e-01 - 4.6e-01	6.4e-01 - 6.7e-01	5.9e-01 - 6e-01
R-hat	1e+00	1e+00	1e+00	1e+00	1e+00
Bulk ESS	1.8e+03	1.7e+03	1.9e+03	2.3e+03	4.2e+03
Tail ESS	3e+03	2.5e+03	2.9e+03	3.2e+03	3.9e+03
BCI					
Estimate	1.90e-01	-2.20e-02	6.70e-01	4.10e-01	8.10e-01
Estimation error	4.70e-02	4.50e-03	3.50e-02	4.10e-03	2.00e-03
95% interval	9.6e-02 - 2.8e-01	-3.1e-02 - -1.3e-02	6e-01 - 7.4e-01	4e-01 - 4.2e-01	8.1e-01 - 8.2e-01
R-hat	1e+00	1e+00	1e+00	1e+00	1e+00
Bulk ESS	4.2e+02	3.2e+03	1.3e+03	3.2e+03	3.7e+03
Tail ESS	8.2e+02	3.2e+03	2e+03	3.7e+03	3.9e+03

Spatial analyses

”Most abundant species” are species with more than 3,000 individuals.

The relatively low proportion of species which do not have a significant Moran’s I test or do not significantly exhibit a higher inter- than intraspecific variation locally can be explained by the low abundances of rare species which represent the majority of species.

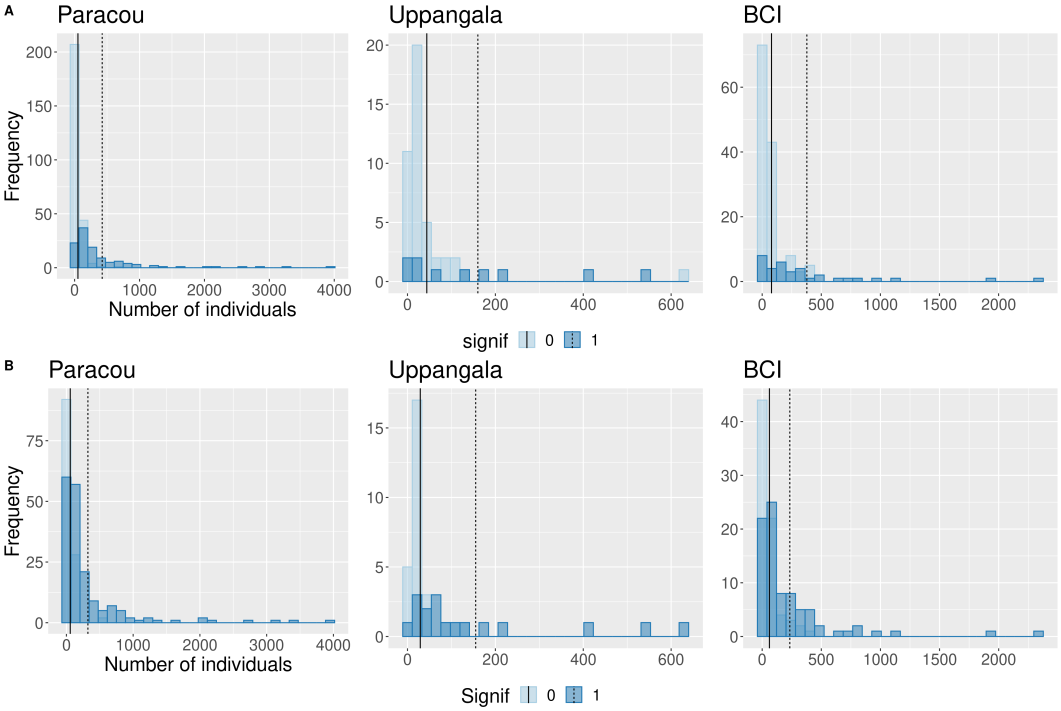


Figure 57: Histograms of the abundances of species which present a significant (dark blue) or insignificant (light blue) Moran’s I test (upper panels) and semivariance comparison test (bottom panels). The dotted lines represent the mean abundance across species with significant (plain) and insignificant (dashed) test in each case. Using a simple generalized linear model with a logit link function, we also showed that the abundance of species is a significant predictor of test significance in both cases (McFadden’s R-squared value = 0.29 for Moran’s I and 0.17 for semivariance comparison for Paracou, 0.11 and 0.25 for Uppangala, 0.19 and 0.13 for BCI; p-value of the effect of abundance on significance = 6e-12 and 5.8e-07 for Paracou, 0.036 and 0.015 for Uppangala, 2.8e-05 and 0.00016 for BCI).

Spatial autocorrelation in undisturbed plots in the Paracou site

One of our main hypotheses was that since many environmental variables are spatially structured and that tree growth is largely influenced by environmental variables, tree growth should be spatially structured. Our analysis using Moran’s I test showed that tree growth was indeed spatially structured at our study sites. The Paracou dataset offers the opportunity to test this hypothesis further. Indeed, some plots were disturbed in the early eighties, creating artificial gaps, whereas others were not disturbed. As the creation of gaps results in a strong spatial structure of the light available under the canopy, we hypothesized that growth should be less structured in plots that were not disturbed.

Considering the undisturbed plots only, the proportion of individuals of species with a significant Moran’s I test was 55%, much lower than when including the disturbed plots (79%, see main text, Table 5; Table 13). This corroborates our hypothesis that the openness of the canopy

Table 13: Spatial autocorrelation of the growth of conspecific individuals in the undisturbed plots of the Paracou site. Shown are the proportion of species, and of corresponding individuals, in %, for which individual growth was significantly spatially autocorrelated, or not significantly spatially autocorrelated. The spatial autocorrelation of individual growth was tested using Moran's I index.

	Significant	**Not significant**
% Species	18.1	81.9
% Individuals	54.7	45.3

Table 14: Comparison of local intra- and interspecific variability in individual growth for three tropical forest sites, when controlling for species abundance. See main text. Semivariances with heterospecifics were here computed by sampling a maximum of 10 individuals per species.

	Intraspecific variability $<$ Interspecific variability (i)	**Intraspecific variability $\sim$ Interspecific variability (ii)**	**Intraspecific variability $>$ Interspecific variability (iii)**
Paracou			
% Species	60.7	38.3	1
% Individuals	86.7	12	1.26
Uppangala			
% Species	42.2	55.6	2.22
% Individuals	64.2	17.4	18.4
BCI			
% Species	59.7	39	1.26
% Individuals	88.7	10.7	0.516

triggered important spatial structure in disturbed plots due to light gaps, and as in these gaps, trees tend to grow faster, the spatial structure of growth is stronger.

Spatial autocorrelation in BCI using smaller stems

In order to be able to compare all three datasets together, we removed all stems that had a DBH inferior to 10 cm in the BCI inventories, which include all stems with DBH $\geq$ 1 cm. We replicated our analysis on the spatial autocorrelation of tree growth in the complete dataset and found that the spatial structure in individual growth was even more significant.

Variance comparison using a sample

To control for a potential effect of species abundance on the values of semivariances with heterospecifics, we replicated the analysis (see main text, Table 6) by computing the semivariances with heterospecifics by sampling a maximum of ten individuals per species. The results were qualitatively unchanged (Table 14).

Appendices of Chapter 2

Appendix 1: Alternative implementations of mortality and fecundity

To test the robustness of our results to the choices made in building the community dynamics simulator, we implemented alternative ways to simulate mortality and fecundity. For mortality, we explored the three following approaches: (i) the one percent less performing individuals in the landscape die at each timestep, henceforth denoted *deterministic mortality*; (ii) one percent of the individuals die at each timestep, and the probability of each individual to die is proportional to its performance, henceforth denoted *stochastic mortality*; (iii) the probability θ_{ij} of each individual j to die is computed as a function of its performance, $\theta_{ij} = \text{logit}^{-1}(\text{logit}(0.01) - 0.5 \times p_{ij})$, henceforth denoted *logistic stochastic mortality*. Death events are then drawn in a binomial distribution $B(n_s, \theta)$ with θ the vector of all θ_{ij}. For fecundity, we explored the two following approaches: (i) the number of propagules $prop_{j,t}$ depends on species abundance $A_{j,t}$: $prop_{j,t} = round(0.5 \times A_{j,t})$, henceforth denoted the *abundance-dependent fecundity*; or (ii) each species present in the community produces ten offspring per timestep, henceforth denoted the *fixed fecundity*. Results obtained with *deterministic mortality* and *abundance-dependent fecundity* are presented in the main text, and we present below the results with other mortality and fecundity alternatives (Fig. 58 to Fig. 67).

Deterministic mortality **and** ***fixed fecundity***

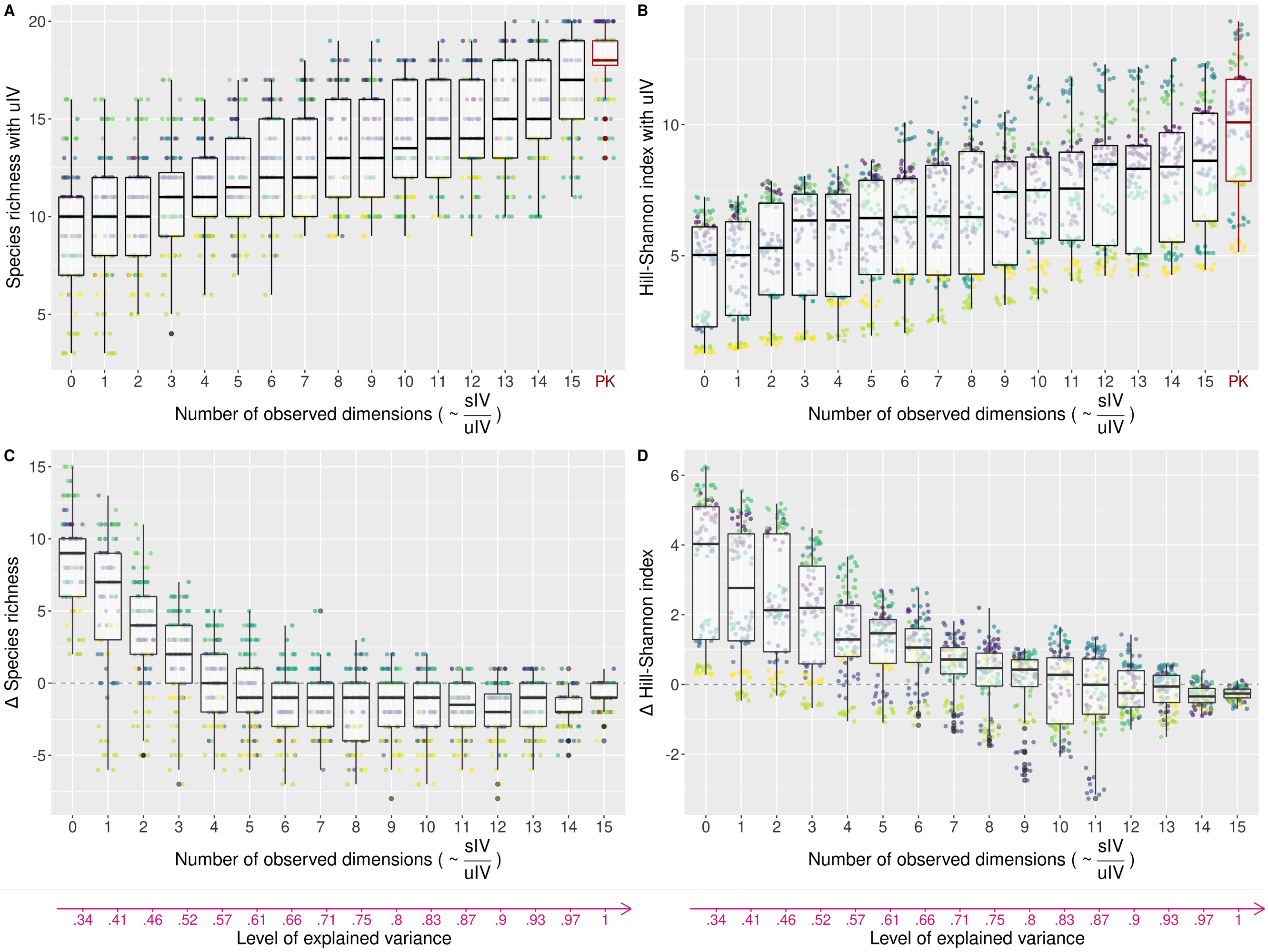


Figure 58: Effect of the structure of individual variation on community diversity. Each point represents the diversity, either computed as the species richness – left panels – or the Hill-Shannon diversity index – right panels – of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 20 of main text) depicted with the pink arrow at the bottom. The top panels show the final community diversity obtained with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in the final community diversity obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher diversity when adding unstructured IV. Results shown here were obtained with a *deterministic mortality* and a *fixed fecundity*.

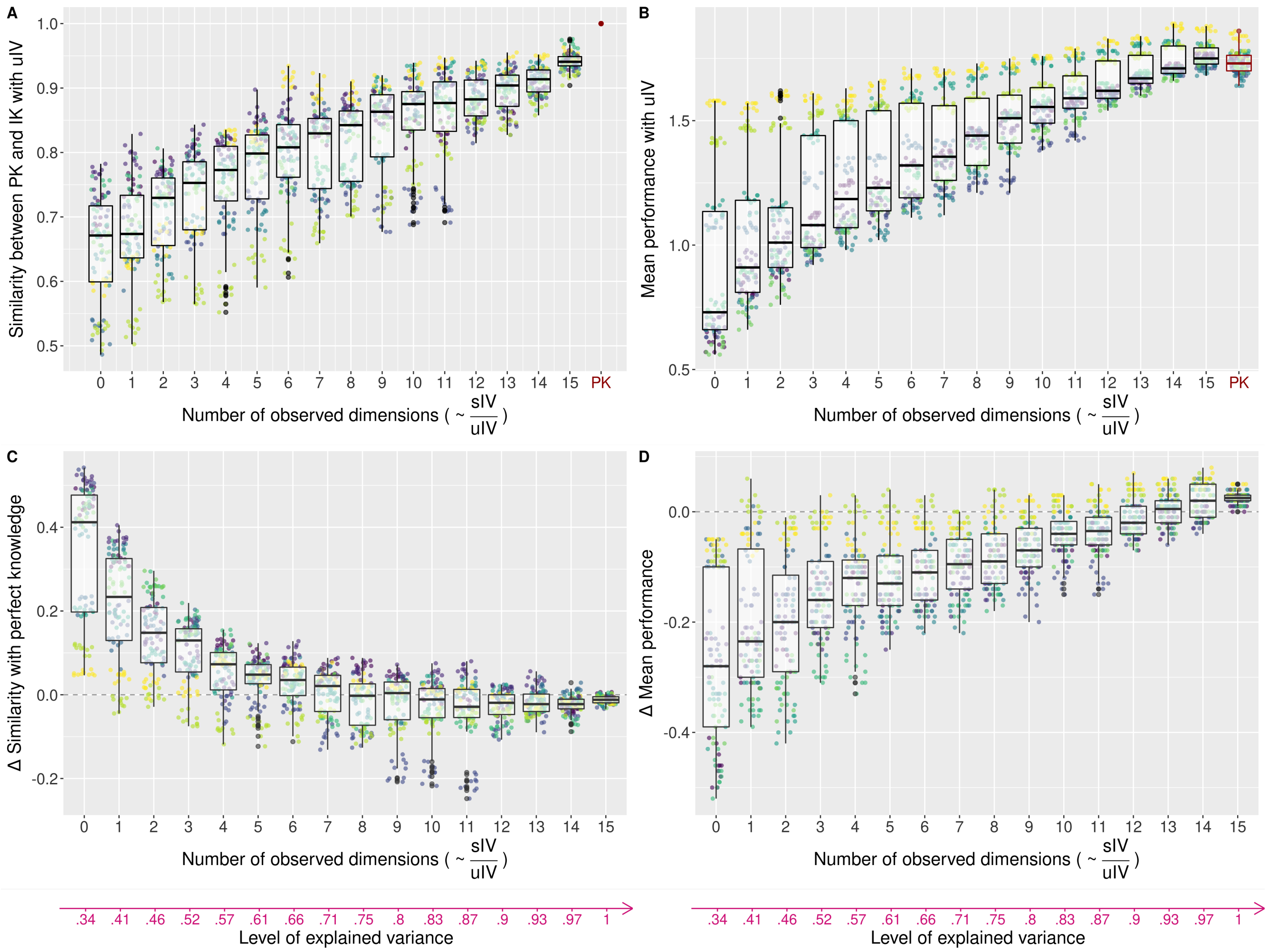


Figure 59: Effect of the structure of individual variation on the similarity in final species abundances between models and on the of the final communities. Each color represents an $E \times S$ configuration. For the similarity - left panels -, each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. The top panels show these two metrics for communities simulated with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in these metrics for communities obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher similarity or mean performance when adding unstructured IV, respectively. Results shown here were obtained with a *deterministic mortality* and a *fixed fecundity*.

Stochastic mortality and *abundance-dependent fecundity*

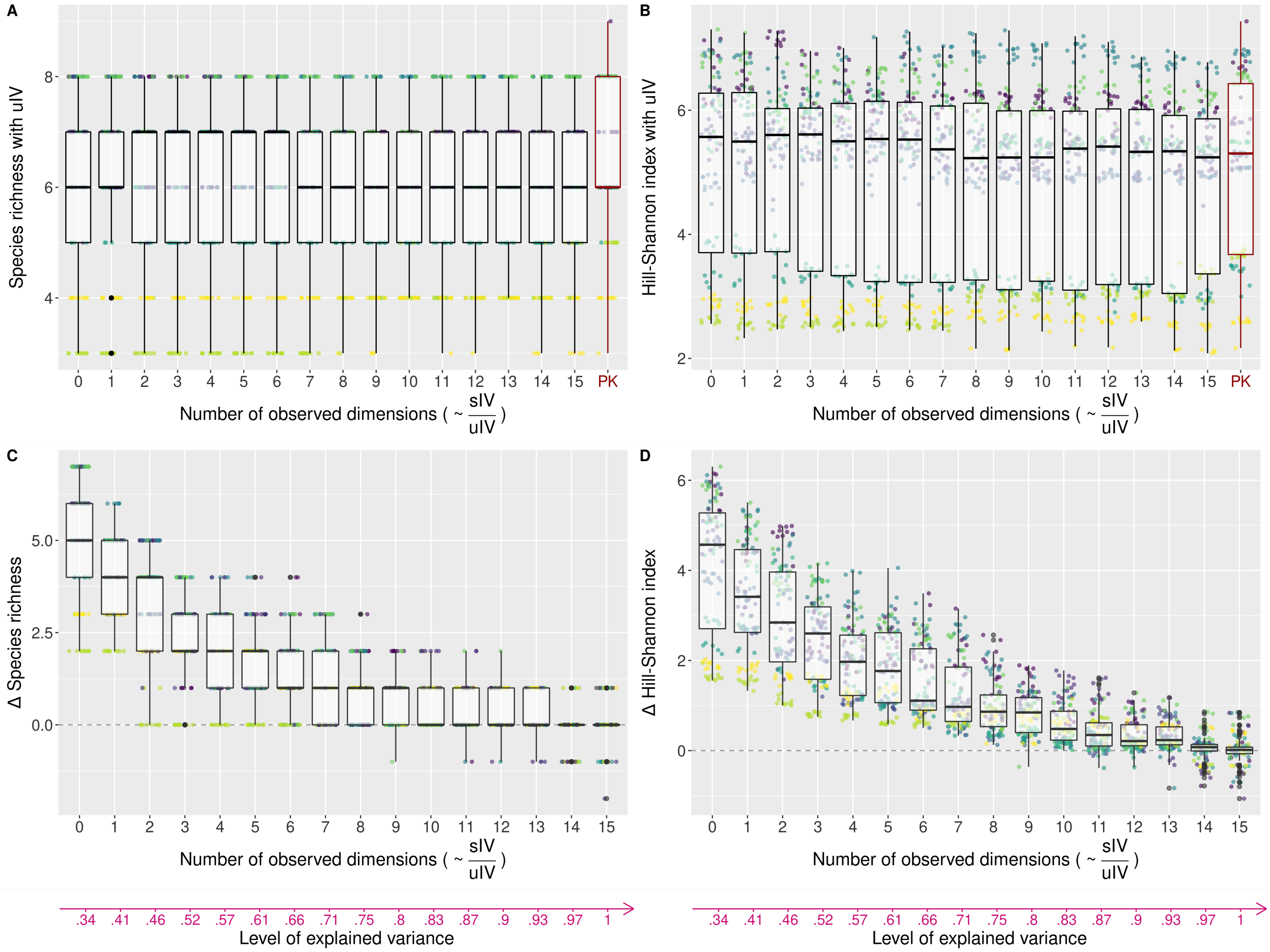


Figure 60: Effect of the structure of individual variation on community diversity. Each point represents the diversity, either computed as the species richness – left panels – or the Hill-Shannon diversity index – right panels – of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 20 of main text) depicted with the pink arrow at the bottom. The top panels show the final community diversity obtained with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in the final community diversity obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher diversity when adding unstructured IV. Results shown here were obtained with a *stochastic mortality* and an *abundance-dependent fecundity*.

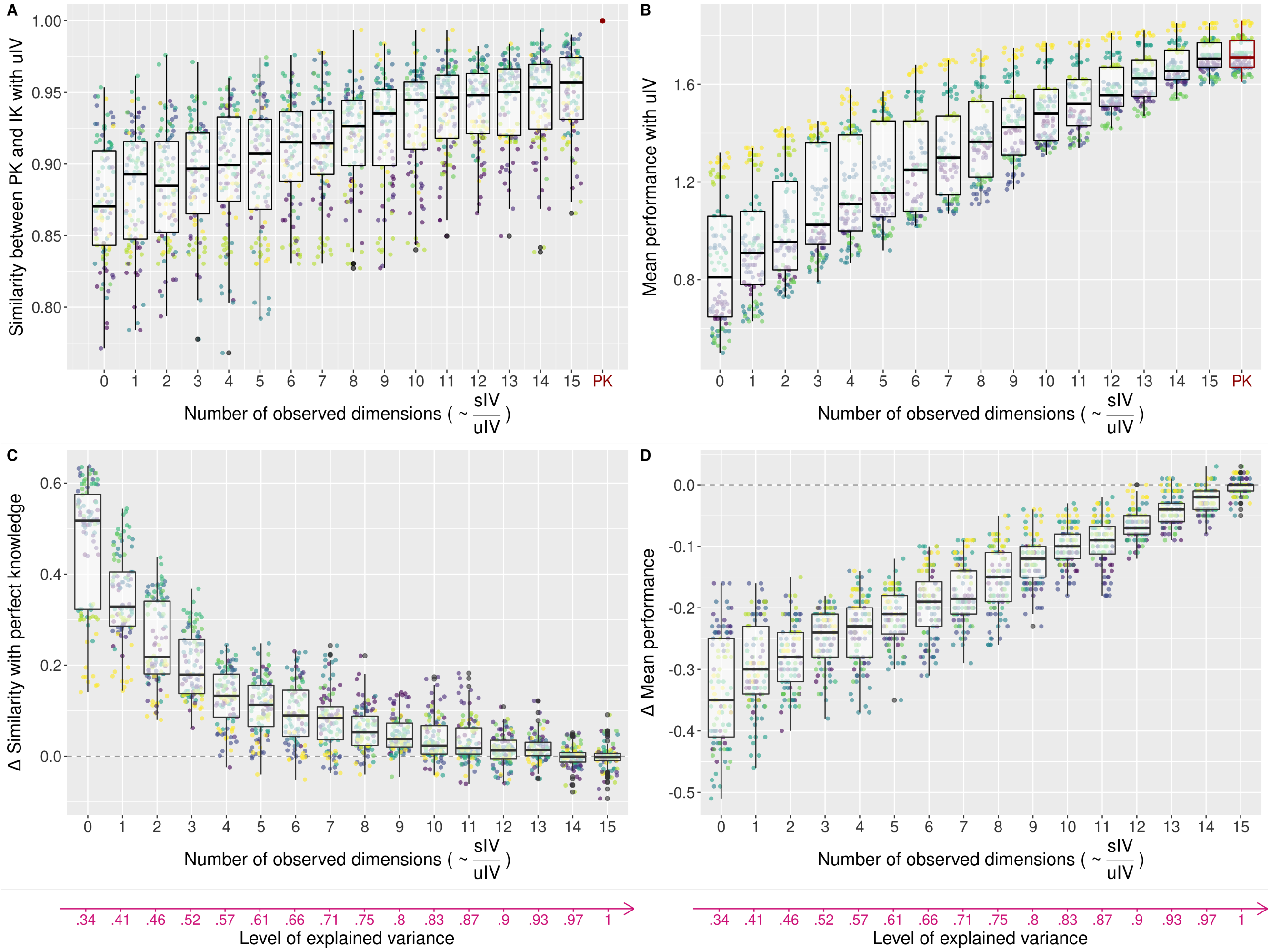


Figure 61: Effect of the structure of individual variation on the similarity in final species abundances between models and on the of the final communities. Each color represents an $E \times S$ configuration. For the similarity - left panels -, each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. The top panels show these two metrics for communities simulated with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in these metrics for communities obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher similarity or mean performance when adding unstructured IV, respectively. Results shown here were obtained with a *stochastic mortality* and an *abundance-dependent fecundity*.

Stochastic mortality and *fixed fecundity*

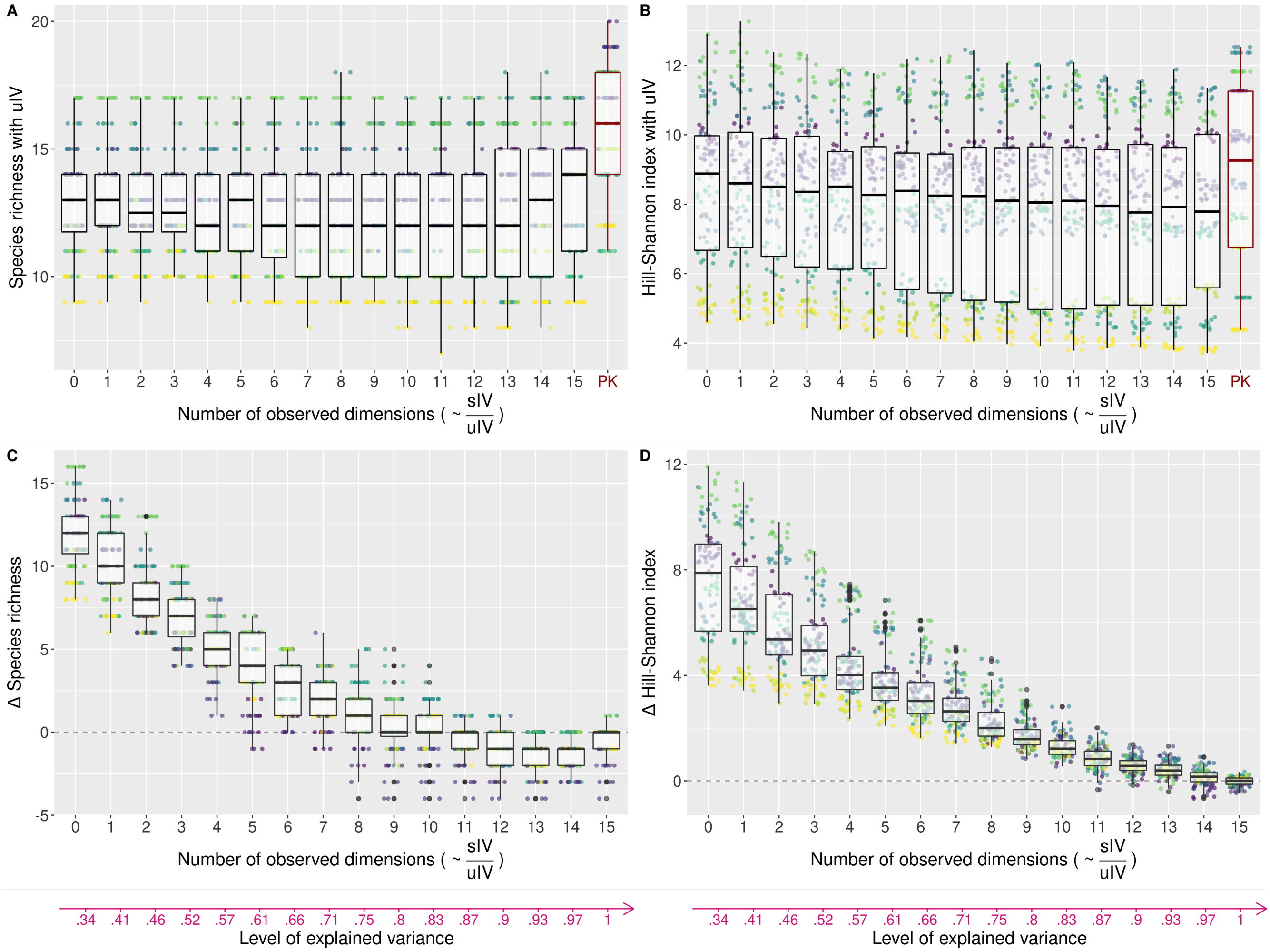


Figure 62: Effect of the structure of individual variation on community diversity. Each point represents the diversity, either computed as the species richness – left panels – or the Hill-Shannon diversity index – right panels – of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 20 of main text) depicted with the pink arrow at the bottom. The top panels show the final community diversity obtained with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in the final community diversity obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher diversity when adding unstructured IV. Results shown here were obtained with a *stochastic mortality* and a *fixed fecundity*.

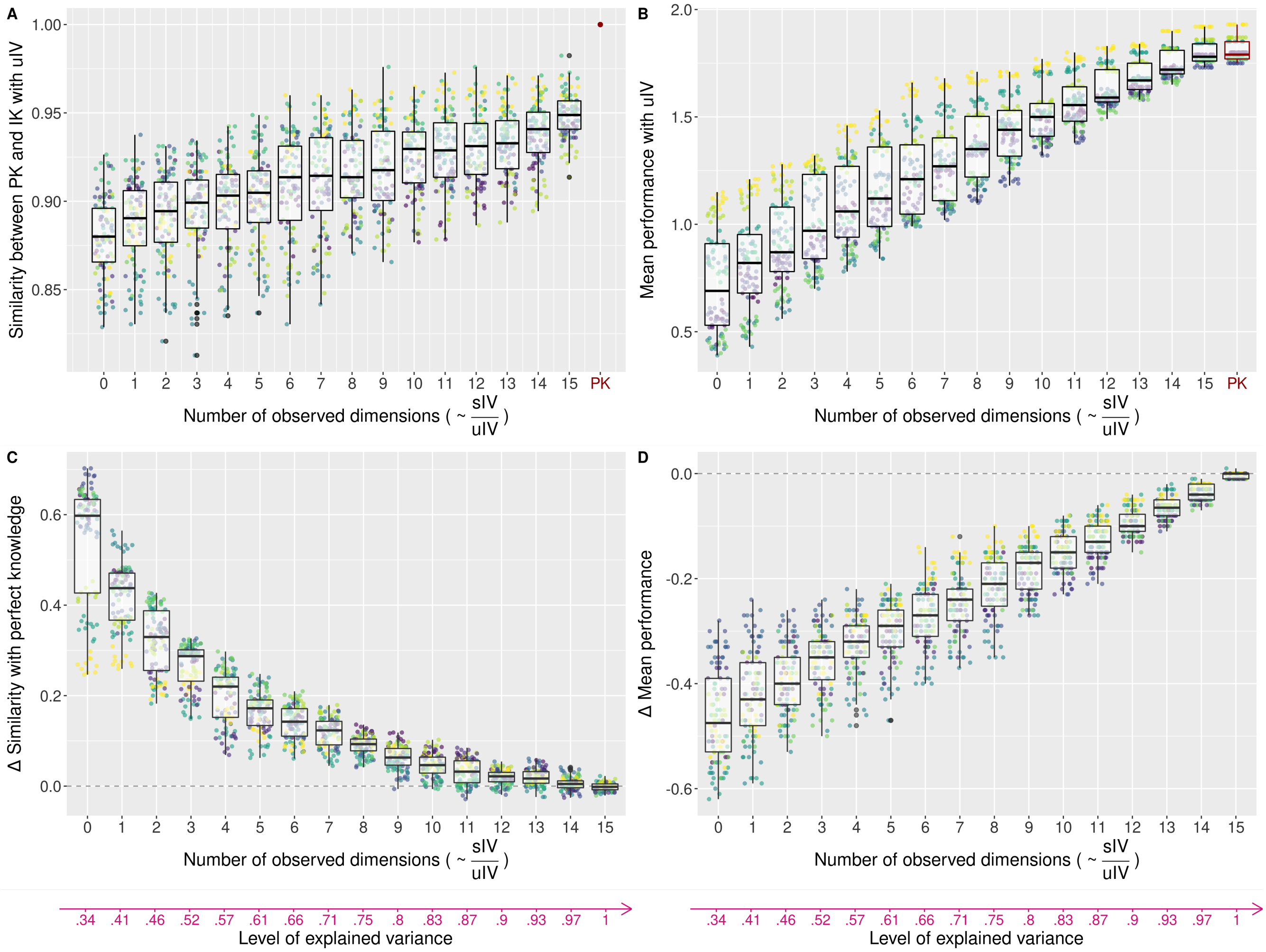


Figure 63: Effect of the structure of individual variation on the similarity in final species abundances between models and on the of the final communities. Each color represents an $E \times S$ configuration. For the similarity - left panels -, each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. The top panels show these two metrics for communities simulated with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in these metrics for communities obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher similarity or mean performance when adding unstructured IV, respectively. Results shown here were obtained with a *stochastic mortality* and a *fixed fecundity*.

Logistic stochastic mortality **and** ***abundance-dependent fecundity***

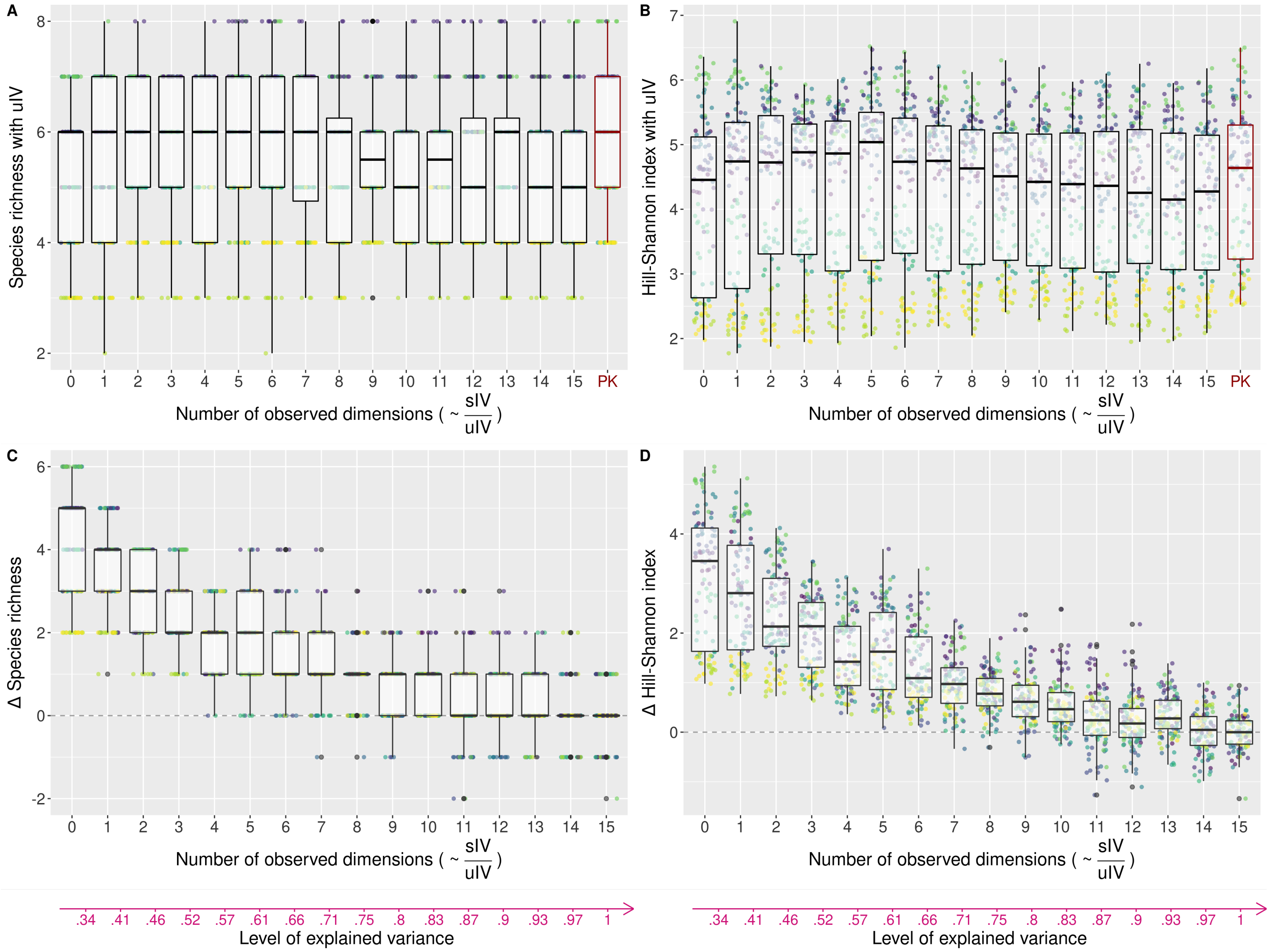


Figure 64: Effect of the structure of individual variation on community diversity. Each point represents the diversity, either computed as the species richness – left panels – or the Hill-Shannon diversity index – right panels – of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 20 of main text) depicted with the pink arrow at the bottom. The top panels show the final community diversity obtained with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in the final community diversity obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher diversity when adding unstructured IV. Results shown here were obtained with a *logistic stochastic mortality* and an *abundance-dependent fecundity*.

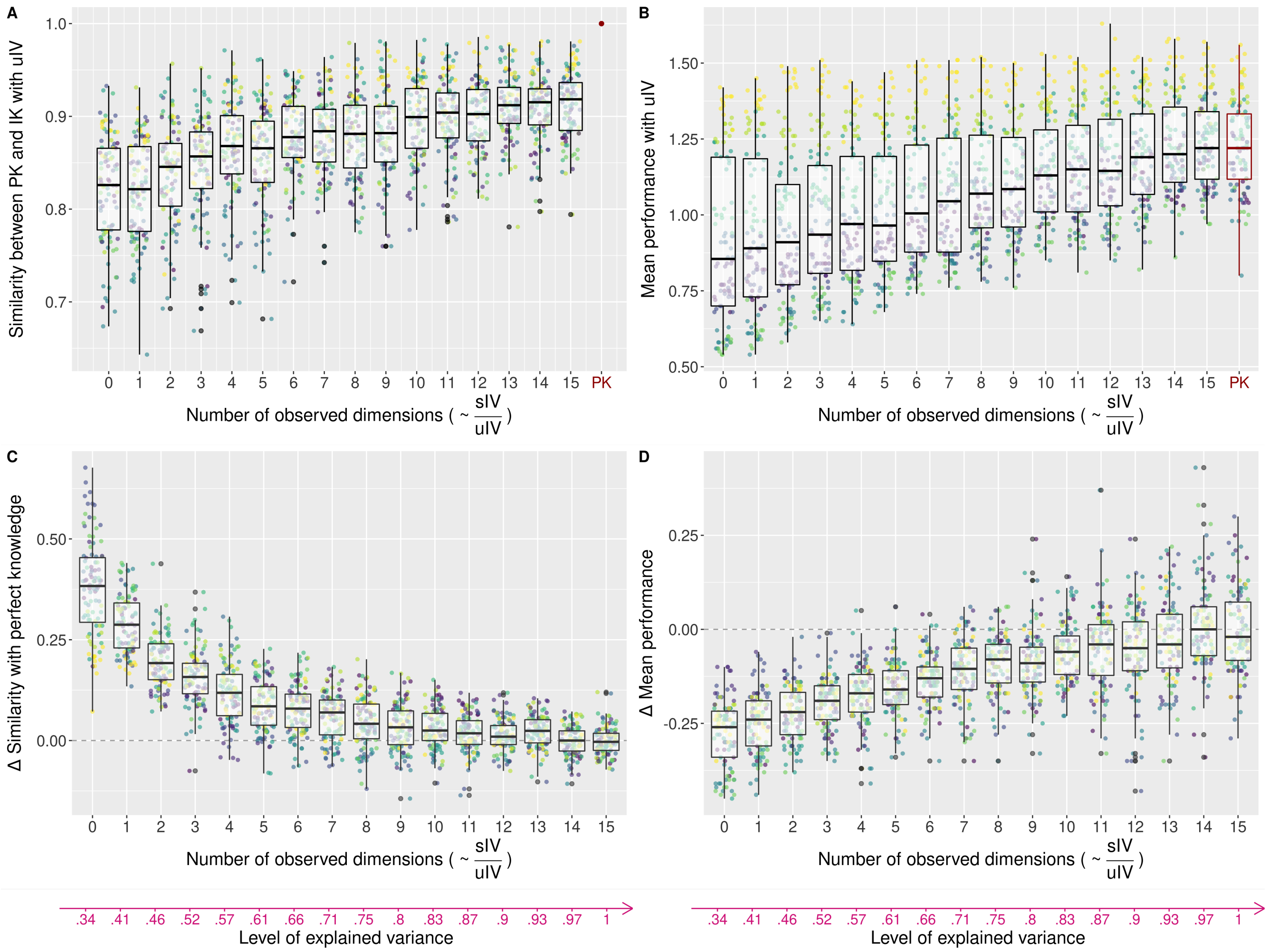


Figure 65: Effect of the structure of individual variation on the similarity in final species abundances between models and on the of the final communities. Each color represents an $E \times S$ configuration. For the similarity - left panels -, each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. The top panels show these two metrics for communities simulated with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in these metrics for communities obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher similarity or mean performance when adding unstructured IV, respectively. Results shown here were obtained with a *logistic stochastic mortality* and an *abundance-dependent fecundity*.

Logistic stochastic mortality **and** ***fixed fecundity***

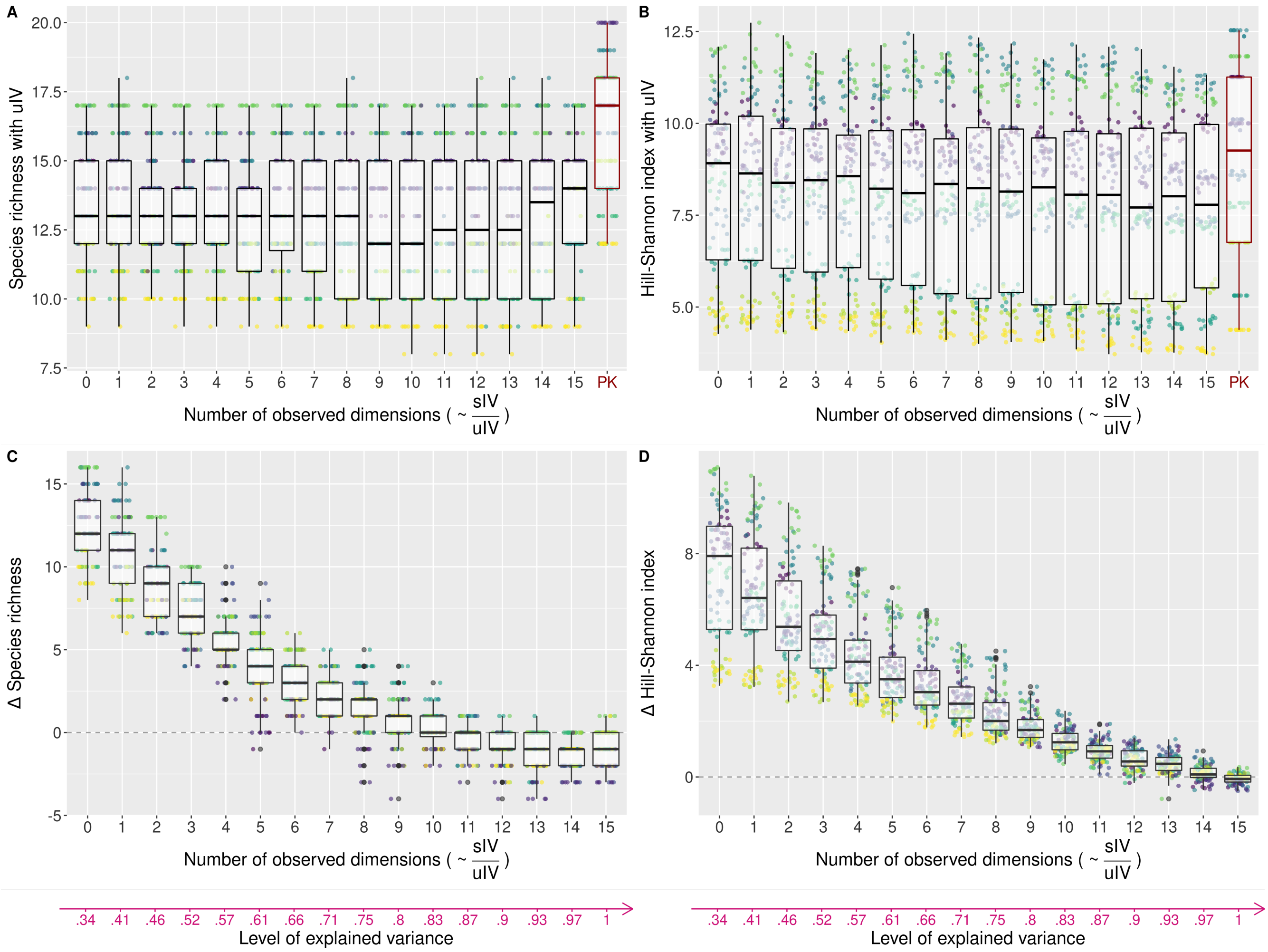


Figure 66: Effect of the structure of individual variation on community diversity. Each point represents the diversity, either computed as the species richness – left panels – or the Hill-Shannon diversity index – right panels – of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 20 of main text) depicted with the pink arrow at the bottom. The top panels show the final community diversity obtained with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in the final community diversity obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher diversity when adding unstructured IV. Results shown here were obtained with a *logistic stochastic mortality* and a *fixed fecundity*.

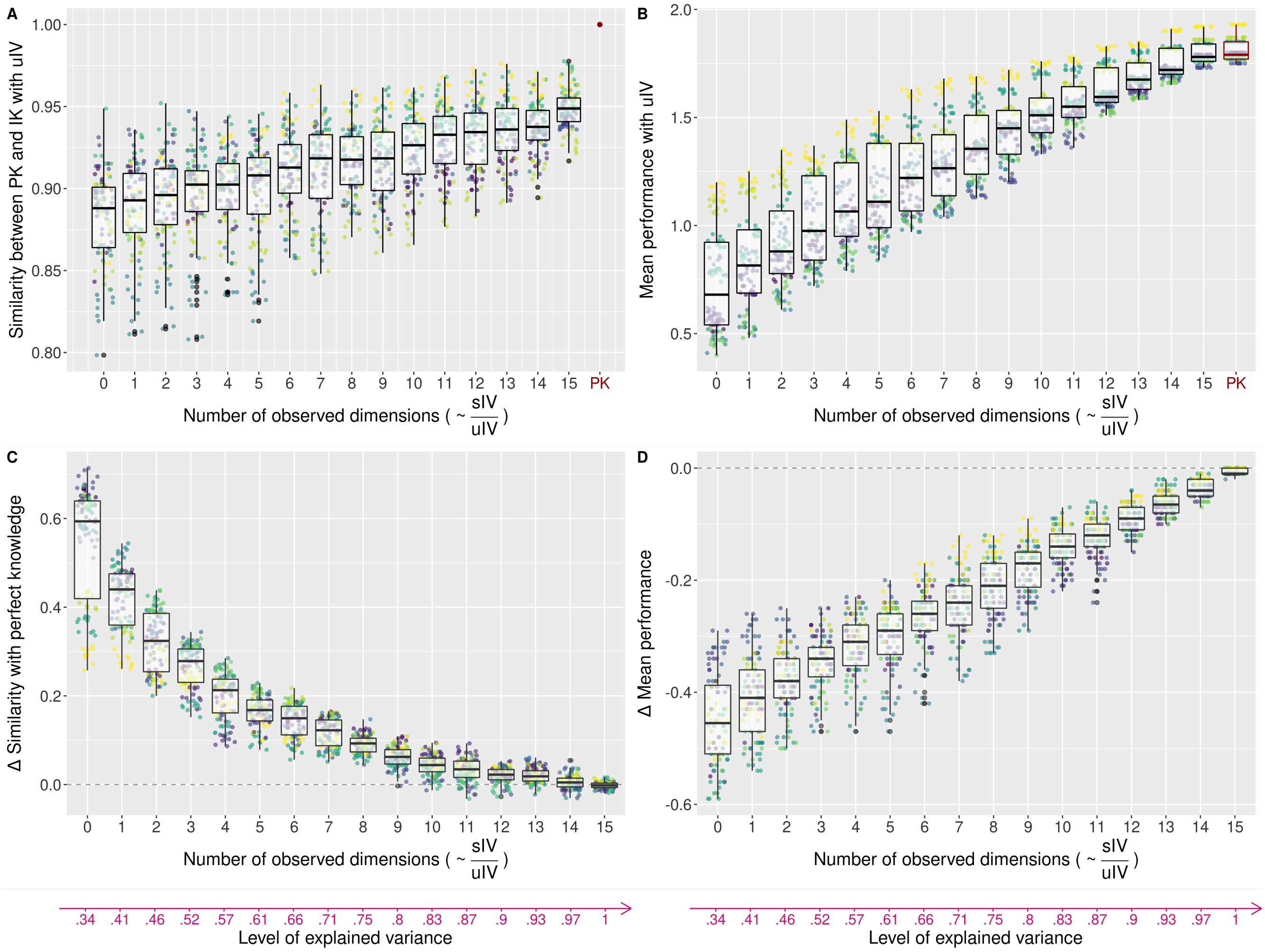


Figure 67: Effect of the structure of individual variation on the similarity in final species abundances between models and on the of the final communities. Each color represents an $E \times S$ configuration. For the similarity - left panels -, each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. The top panels show these two metrics for communities simulated with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in these metrics for communities obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher similarity or mean performance when adding unstructured IV, respectively. Results shown here were obtained with a *logistic stochastic mortality* and a *fixed fecundity*.

Appendix 2: Stability of the simulations

We would expect the simulations made with unstructured IV in individual performance to be characterized by significantly different final communities with various species abundance distributions (unstable coexistence, Hubbell 2001). However, all three models of individual performance produced communities with relatively similar final species abundance distribution, and this stability was actually even lower for the *Perfect knowledge model* (Fig. 68). This was explained by the fact that with the *Perfect knowledge model*, rare species can be maintained in the community but with a high dependence on initial conditions. On the contrary, *Imperfect knowledge models* enable mainly species with abundant suitable habitat to persist in the community, and are therefore less sensitive to initial conditions. With many observed dimensions, the *Imperfect knowledge models without uIV* even become less stable than the *Imperfect knowledge models with uIV*. As the *Imperfect knowledge models without uIV* approach the *Perfect knowledge model*, it enables more rare species to be maintained, with a high dependence on initial conditions.

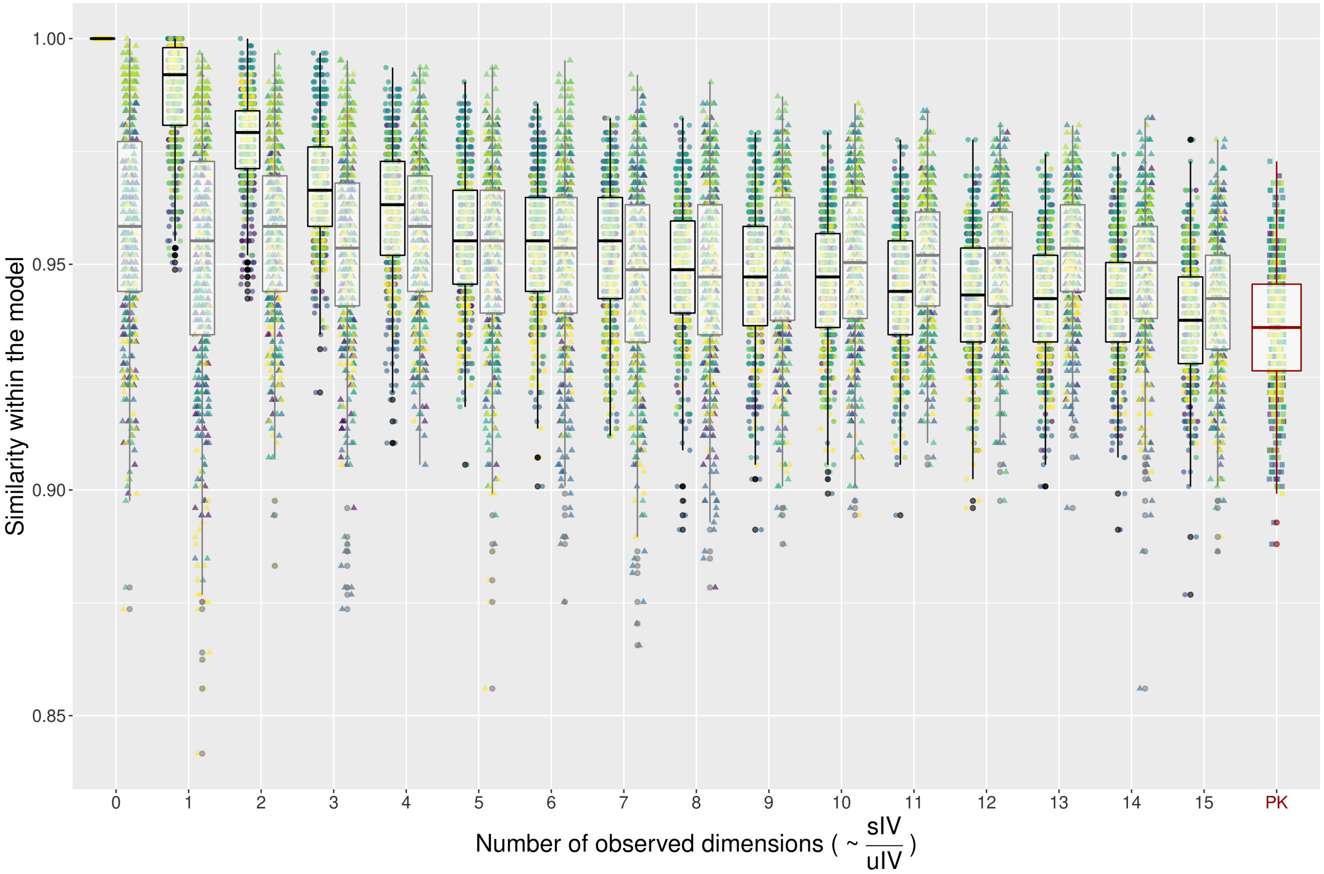


Figure 68: Effect of the structure of individual variation on the stability of the community composition within models. Each point represents the pairwise percentage similarity of the species abundances of the final community of two repetitions of the same model with the same $E \times S$ configuration. Each color represents a $E \times S$ configuration (45 points per color). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. At a given number of observed dimensions, the black boxplot on the left corresponds to communities simulated with the *Imperfect knowledge model without uIV* while the gray boxplot on the right corresponds to communities simulated with the *Imperfect knowledge model with uIV*, except on the far right (PK) where the red boxplot, represents communities simulated with the *Perfect knowledge model*. Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity*.

Appendix 3: Role of suboptimal species depending on the implementation of mortality and fecundity

With some particular environments and species optima ($E \times S$ configuration), some species that are theoretically not winners in the landscape, i.e. that can be outperformed by another species in any site, can be maintained. We refer to these species as suboptimal species. These suboptimal species have optima that are similar to the optimum of a dominant species (or theoretical winner) and their performance at the optimum is therefore high (although suboptimal). Suboptimal species present on sites close to the optimum of an actual dominant species, can have a higher performance than actual dominant species on some other sites.

With *deterministic mortality*, only a determined number of the less performant individuals die at each iteration. Therefore, individuals belonging to dominant species die rather than individuals of suboptimal species, enabling a high level of coexistence even when there are only few theoretical winners. As a result, the communities simulated with the *Perfect knowledge model* (or the *Imperfect knowledge model* with fifteen dimensions) can be outperformed in terms of mean performance because suboptimal species can persist (Fig. 22B of the main text). However, this effect varies depending on the way mortality was implemented.

With *stochastic mortality*, the difference in mean performance between communities simulated with or without unstructured IV tends to zero as unstructured IV decreases. With *deterministic mortality* however, the difference is always higher than with *stochastic mortality*, so that starting from seven observed dimensions, the communities tend to have a higher mean performance with unstructured IV (Fig. 22D of main text). This is due to the number of individuals belonging to suboptimal species. In the case of a *deterministic mortality*, the difference in mean performance between communities simulated with vs. without unstructured IV is tightly negatively related to the difference in the number of individuals belonging to suboptimal species (Fig. 69). Indeed, the number of suboptimal individuals is higher with deterministic than *stochastic mortality* since suboptimal individuals can durably persist as never being among the least performing individuals in the community that are filtered out at each time step (Fig. 70). Moreover, the addition of unstructured IV impacts more negatively the number of individuals of suboptimal species in the case of deterministic rather than *stochastic mortality* (Fig. 71). Indeed, unstructured IV reduces the possibility to generate individuals that durably persists: in average, half of them will have a lower performance with unstructured IV than without, increasing their chance of being filtered out.

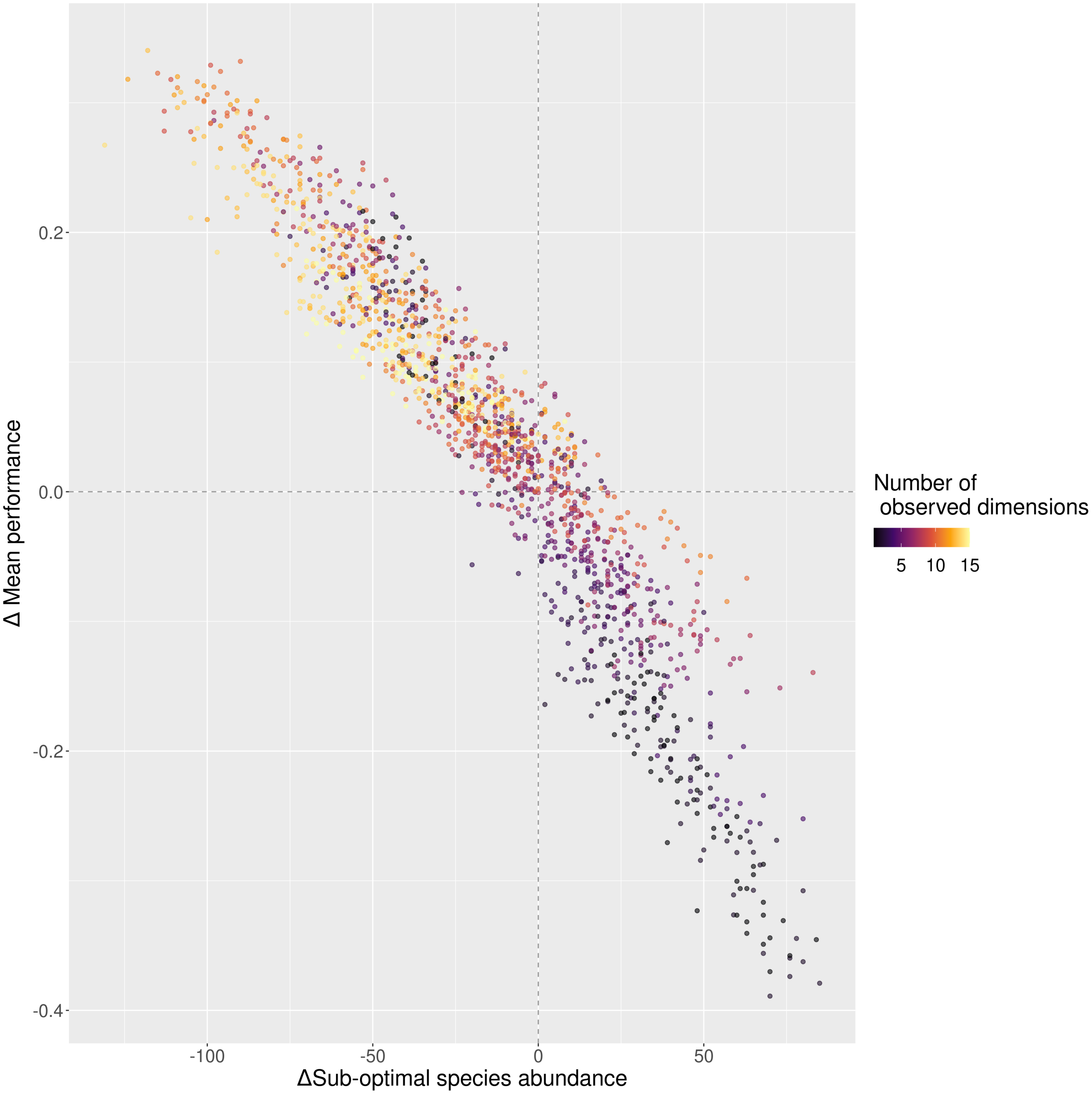


Figure 69: Relationship between the effect of adding unstructured IV on suboptimal species abundances and mean performance. Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity*.

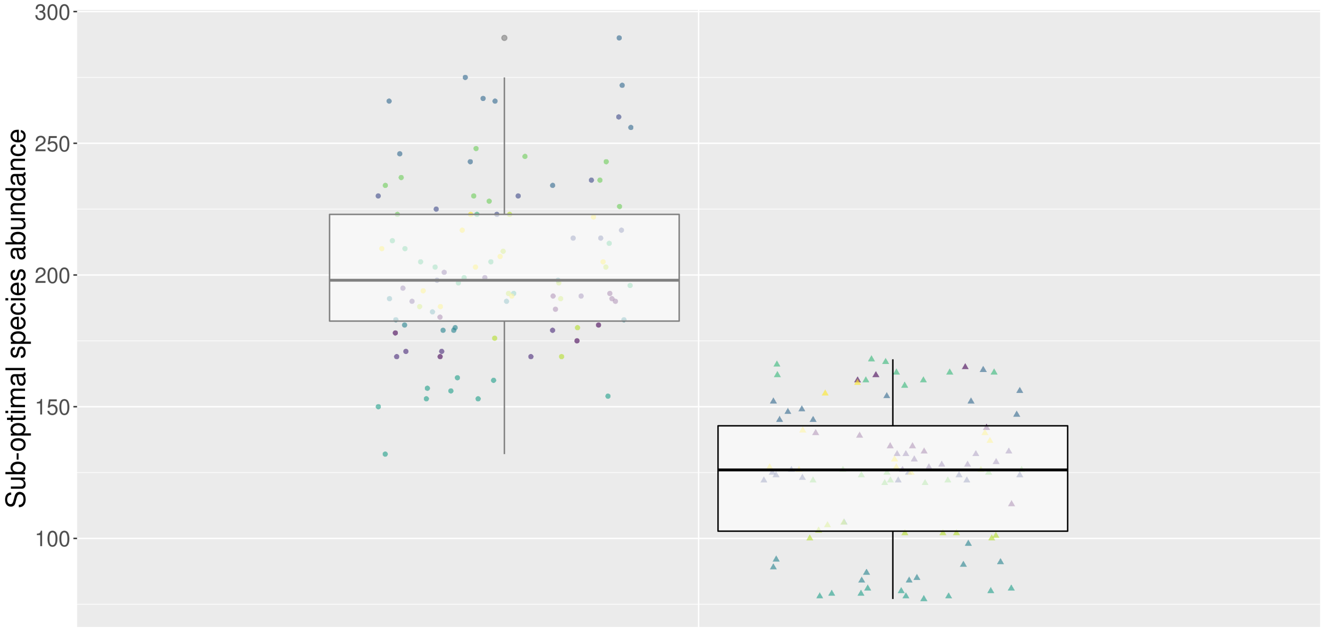


Figure 70: Abundance of suboptimal species in the final communities simulated with deterministic *vs.* *stochastic mortality.* Each point represents the total number of individuals of suboptimal species in the final communities obtained with the *Perfect knowledge model*. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The gray boxplot on the left corresponds to communities simulated with a *deterministic mortality* while the black boxplot on the right corresponds to communities simulated with a *stochastic mortality*. Results shown here were obtained with *abundance-dependent fecundity*.

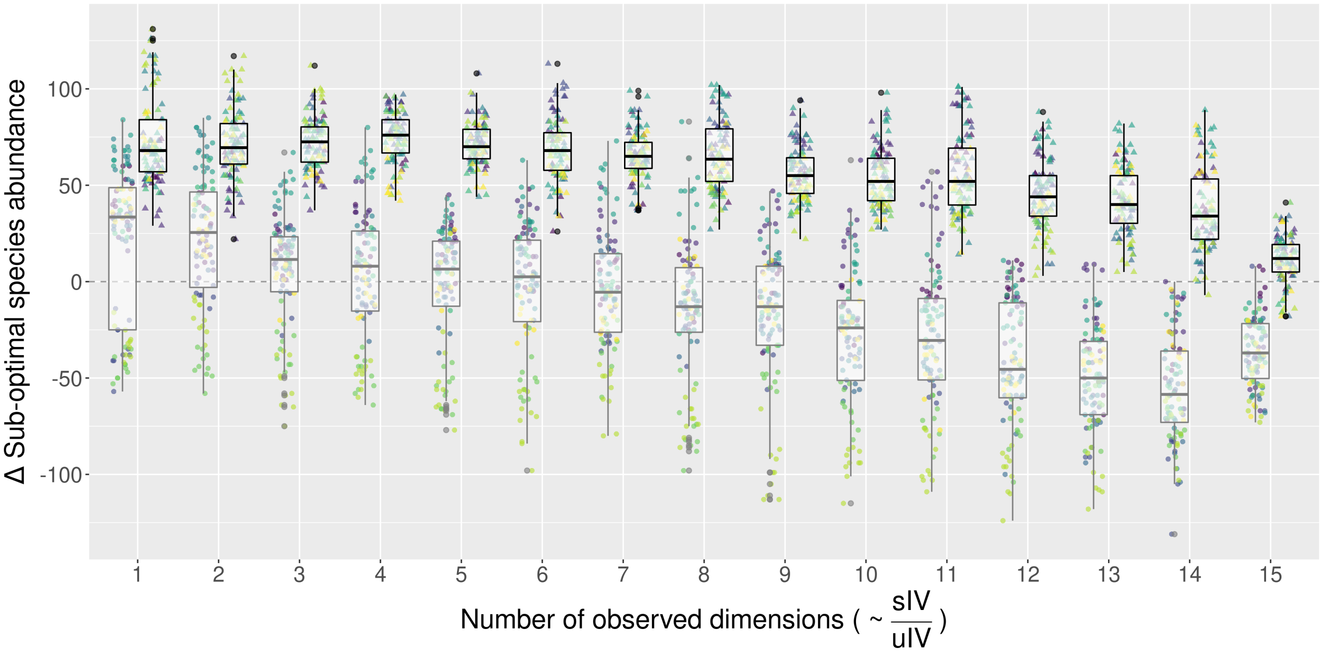


Figure 71: Comparison of the effect of adding unstructured IV on the abundance of suboptimal species between communities simulated with deterministic *vs. stochastic mortality*. Each color represents an $E \times S$ configuration. Each point represents the difference between the abundance of suboptimal species in the final communities obtained with the same $E \times S$ configuration and the same initial conditions (ten points per color), but simulated with the *Imperfect knowledge models with vs. without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher abundance of suboptimal species when adding unstructured IV. At a given number of observed dimensions, the gray boxplot on the left corresponds to communities simulated with a *deterministic mortality* while the black boxplot on the right corresponds to communities simulated with a *stochastic mortality*. Results shown here were obtained with *abundance-dependent fecundity*.

Appendix 4: Comparisons between communities simulated with the *Imperfect knowledge models without uIV* and with the *Perfect knowledge model*

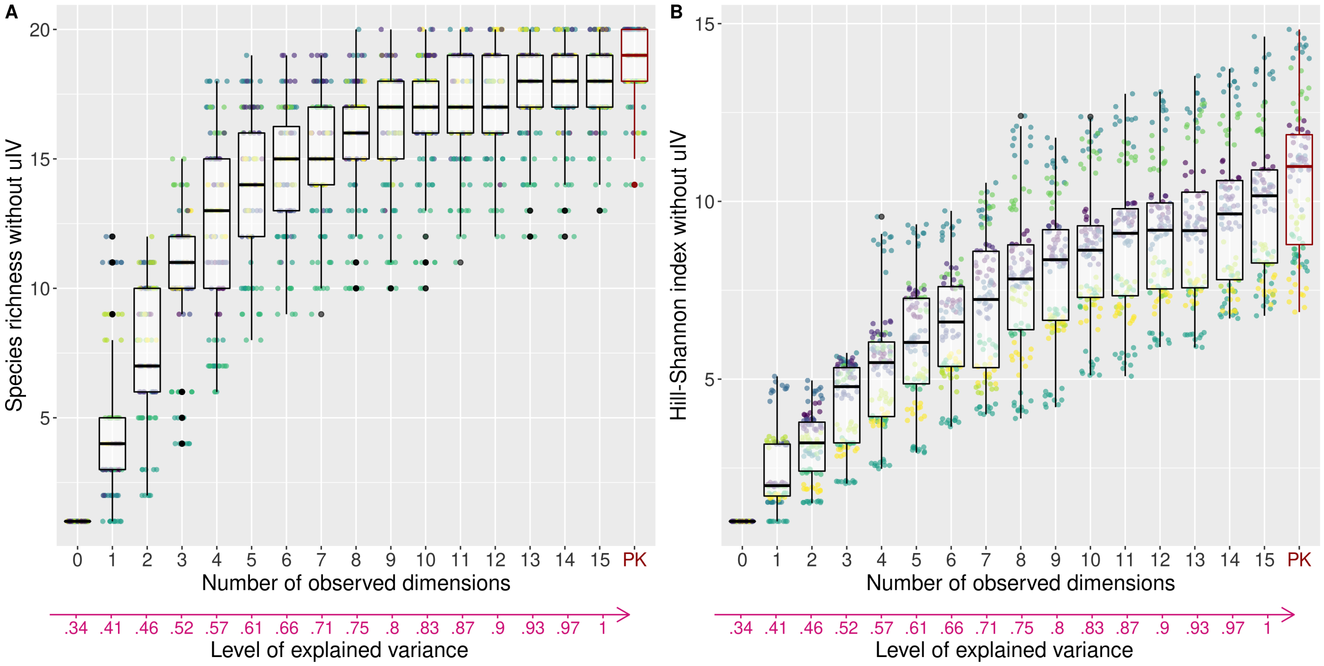


Figure 72: Effect of the number of observed environmental dimensions on community diversity. Each point represents the diversity, either computed as the species richness (A) or the Hill-Shannon diversity index (B) of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 20 of main text) depicted with the pink arrow at the bottom. The vertical axis corresponds to the final species richness obtained with the *Imperfect knowledge models without uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). Comparing the *Imperfect knowledge models without uIV* with the *Perfect knowledge model* is useful to examine the effect of the reduction of the number of observed dimensions on species richness. Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity.*

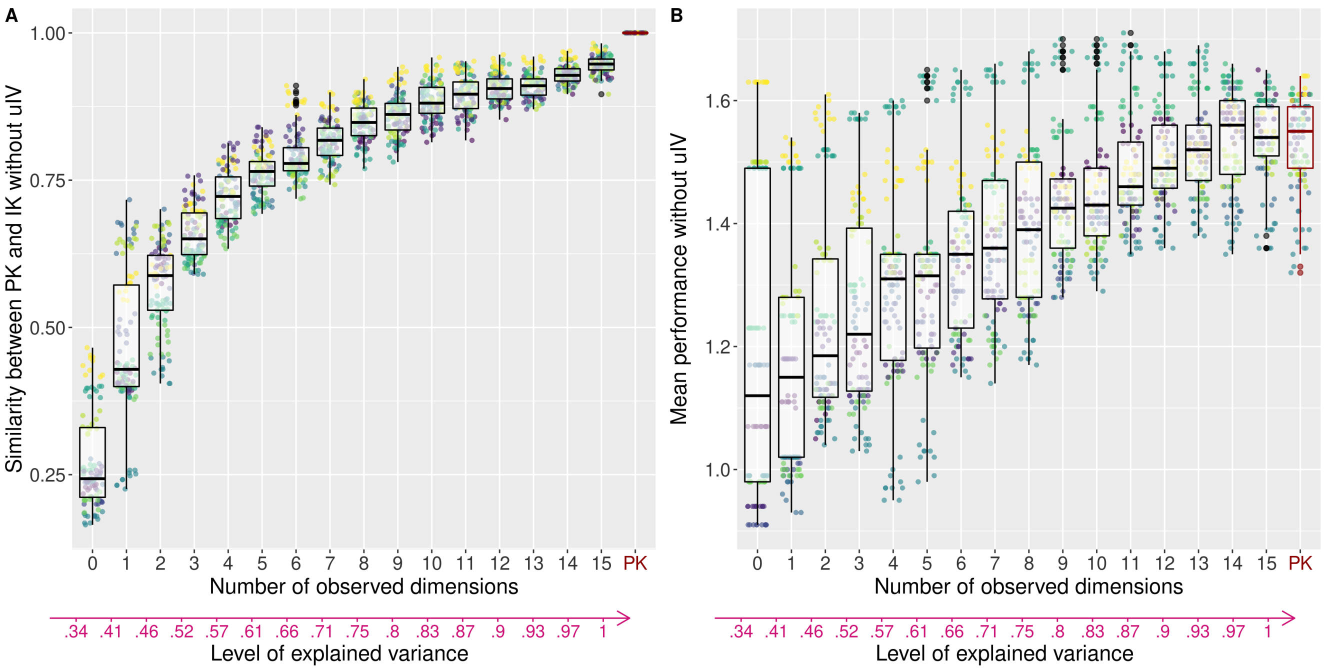


Figure 73: Effect of the number of observed environmental dimensions on the similarity in final species abundances between models and on the site sorting. Each color represents an $E \times S$ configuration. For the similarity (A), each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models without uIV* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. These two metrics were computed for communities simulated with the *Imperfect knowledge models without uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity*.

Appendices of Chapter 3

This appendix includes technical background for simulation and implementation of the hybrid model (eq. HY). To reduce the need for cross-referencing with the main text, we repeat some of the basic model elements here.

Model description

Consider a community of individuals that contribute to local population change through their differing birth rates that determine local crowding, which, in turn, drives density-dependent survival. They contribute to landscape population growth through dispersal. The model necessarily operates on discrete individuals, the numbers of which will vary in space and time. In year t, the entire community consists of $i = 1, \ldots, n_t$ individuals of $s = 1, \ldots, S$ species that interact locally over $k = 1, \ldots, K$ neighborhoods, or 'sites'. If there is a large number of species on the landscape, local interactions ('within a site') involve individuals from a subset of the total S species. Individual differences combine species mean responses with additional variation. The environment varies in E dimensions, held in a $K \times E$ matrix $\mathbf{E}$. Species responses are held in a $E \times S$ matrix $\mathbf{S}$ (eq. SK) or, equivalently, in a $S \times S$ covariance matrix $\mathbf{C}$ (eq. SU). At the species level, the response at location k is summarized as $\mathbf{S}'\mathbf{E}_k$, the second factor being row k of $\mathbf{E}$. Large E (many dimensions) is needed to completely specify species responses, which, of course, cannot be fully observed. The $E \times E$ covariance between sites, $\text{Cov}(\mathbf{E}) = \mathbf{V}_\mathbf{E}$, becomes important for the translation of the unobserved variation at the species level to the observable variation among individuals that induces covariance $\mathbf{C}$. We wish to determine how variability among individuals, through known or unknown causes, affects community diversity.

We model continuous variation in individual performance and three sources of stochasticity related to discrete individuals, including i) new offspring, some of which are dispersers, ii) survival, and iii) site locations where dispersing individuals land. Each individual i alive at time t is identified by a label $i[s, k]$ in the time-varying discrete space $(S, K)^{n_t}$. An individual has reproductive potential $h_{i[s,k]} \in [0, \infty)$ that results from $E \times S$ variation as known (eqn SK) or unknown (eqns SU, UU) variation. Reproductive potential is non-negative, because survivors are those for which $h_i > 0$. This reproductive potential, assigned at birth, centers an individual's annual contribution to population growth,

$$g_{i,t} \sim N(h_i, \sigma^2) \tag{3.3}$$

where h_i is an element of the length-$n_{k,t}$ vector $\mathbf{h}_k$ that includes values for individuals of all species at the site, $h_{i[sk]}, s \in 1, \ldots, S$. Surviving individuals subsequently produce round$(g_{i,t})$ offspring each year for as long as they survive. The round$(\cdot)$ function assigns to its argument the nearest integer value. A fraction q of offspring enter the disperser pool. Dispersers are distributed at random across sites. Following birth, the number of non-dispersing individuals of species s at k is

$$n_{sk,t} = \sum_i \text{round}\left(g_{i[s'k']t}(1-q)\right) I(s' = s, k' = k)$$

where $I(\cdot)$ is the identity function that is equal to one when its argument is true and zero otherwise.

There is local density dependence. If local density is below the site capacity C, then all offspring survive. When abundance exceeds C, survival of the surplus individuals declines with local density as a probit function,

$$p_{k,t} = 1 - \Phi\left(\frac{-n_{k,t} + C}{z}\right)$$

where z determines how steeply the function approaches zero survival of the population fraction above C, and $\Phi(\cdot)$ is the standard normal distribution function. Survivors of this density-dependent mortality risk are selected at random from local occupants. The number of survivors from the $n_{k,t} = \sum_s n_{sk,t}$ individuals is

$$P_{k,t} = \begin{cases} n_{k,t} & n_{k,t} \leq C \\ C + \text{round}(p_{k,t}(n_{k,t} - C)) & n_{k,t} > C \end{cases}$$

The survival of each species is proportional to abundance, without regard for species identity,

$$\begin{aligned} \mathbf{R}_{k,t} &\sim \mathit{multinom}(P_{k,t}, \boldsymbol{\theta}_{k,t}) \\ \theta_{(s=1,\ldots,S)k,t} &= n_{sk,t}/n_{k,t} \end{aligned} \tag{3.4}$$

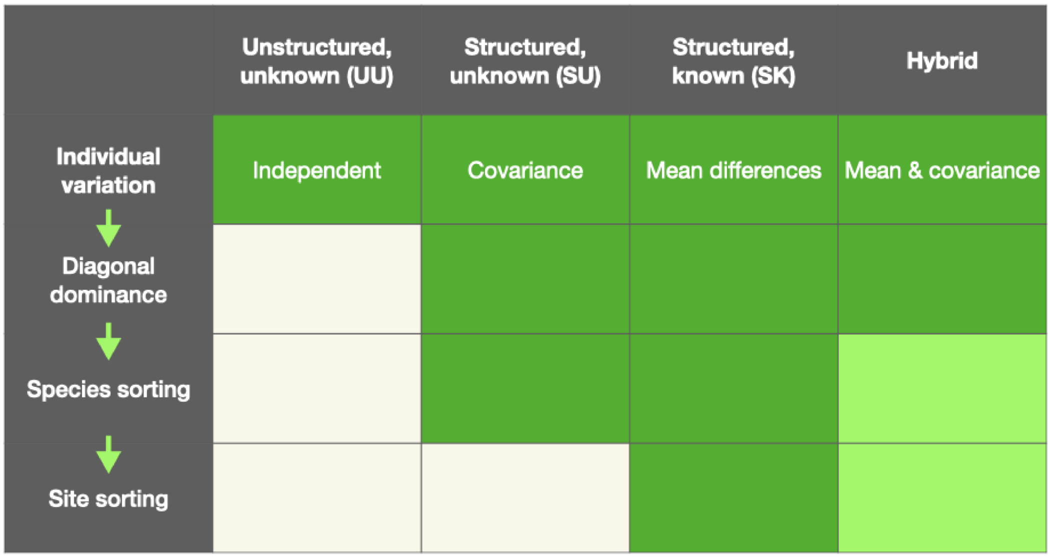
where $\mathbf{R}_{k,t} = [R_{1k,t}, \ldots R_{Sk,t}]$ holds the surviving number of each species. Dispersers are randomly assigned new sites with equal probability,

$$\begin{aligned} d_{s,t} &= \sum_i \text{round}\left(g_{i[s'k]t} \times q\right) I(s' = s) \\ \mathbf{D}_{s,t} &\sim \mathit{multinom}(d_{s,t}, \boldsymbol{\gamma}) \\ \gamma_{(k=1,\ldots,K)} &= 1/K \end{aligned} \tag{3.5}$$

where $d_{s,t}$ is the number of dispersers of species s from all locations, and $\mathbf{D}_{s,t} = [D_{s1,t}, \ldots D_{sK,t}]$ holds the number of individuals of species s assigned to each location k. The updated local abundance for s at k includes survival and births, both local and dispersers,

$$n_{sk,t+1} = R_{sk,t} + D_{sk,t} \tag{3.6}$$

Several features of the three structures are summarized in Fig. 74. Structured, known (SK) responses enter through the mean structure of the model. In practice, this knowledge would never be available, but the SK model exposes the effect of environmental variation that determines the covariance structure between individuals in the structured, unknown (SU) responses. Both SK and SU models have diagonal dominance in their covariance structure ($\mathbf{C}_{ss} > \mathbf{C}_{s's}$ in Fig. 74). In the case of SK, where covariance is not explicit, it is induced by the mean **ES**. Only the SK model exhibits site sorting, because species responses are mapped directly to locations (Fig. 24c and e). Both SK and SU models exhibit species sorting (Fig. 24d) as covariance in simulation aligns with their similar responses in **ES**. Unstructured, unknown (UU) variation adds noise, without structure. The hybrid includes species differences in the mean and observable covariance, thereby combining elements SK and SU.



	Unstructured, unknown (UU)	Structured, unknown (SU)	Structured, known (SK)	Hybrid
Individual variation	Independent	Covariance	Mean differences	Mean & covariance
↓ Diagonal dominance				
↓ Species sorting				
↓ Site sorting				

Figure 74: Model attributes for the main text and the hybrid in this Supplement.

Competitive species and competitive sites

Local sites vary in the productivity they support, and species vary in dominance. The model captures both effects in the site by environment matrix **E** and environment by species matrix **S**. There is a site-by-species suitability map of performance,

$$\mathbf{K} = \mathbf{E}\mathbf{S}$$

which can be used to identify which species has the advantage at each site in the SK model. There is a vector of competitive sites,

$$\bar{\mathbf{k}} = S^{-1}\mathbf{K}\mathbf{1}_S \tag{3.7}$$

where $\mathbf{1}_S$ is the length-S vector of ones. This vector can be used to determine sites of high and low productivity. There is also a vector of competitive species,

$$\bar{\mathbf{s}} = K^{-1}\mathbf{1}'_K\mathbf{K} \tag{3.8}$$

This vector determines species differences in productivity. The site heterogeneity in species performance is

$$\mathbf{v}_K = diag(S^{-1}\mathbf{K}\mathbf{K}' - \bar{\mathbf{k}}\bar{\mathbf{k}}') \tag{3.9}$$

High values mean large differences in species ability to perform on the site. There is also species heterogeneity,

$$\mathbf{v}_S = diag(K^{-1}\mathbf{K}'\mathbf{K} - \bar{\mathbf{s}}\bar{\mathbf{s}}') \tag{3.10}$$

High values mean that sites vary widely in their ability to support a species.

Simulation

In the pseudocode that follows the $E \times n_{kt}$ matrix $\tilde{\mathbf{S}}_{kt} = \mathbf{S}_{[\cdot, i[s,k]t]}$ includes columns of $\mathbf{S}$ corresponding to the species-site labels $i[sk]$ for individuals $i = 1, \ldots, n_{k,t}$ alive at k at time t such that $\tilde{\mathbf{C}}_{k,t} = \tilde{\mathbf{S}}'\mathbf{E}\tilde{\mathbf{S}}$. Also as previously, the tilde notation refers to the individual scale.

1. Specify dimensions and parameter values S, E, K, C, z, q, σ^2, and τ^2 *(e.g.*, Table 15).

2. Generate $E \times S$ matrix $\mathbf{S}$ and $K \times E$ matrix $\mathbf{E}$ with independent elements drawn from $N(0, 1)$.

3. Evaluate landscape variation in the environment, $\mathbf{V_E} = cov(\mathbf{E})$.

4. Initialize sites with equal numbers of individuals from S species. Assign each a lifetime species label that will be inherited by its offspring.

5. The loop over time t includes the following steps:

    (a) Determine births by each individual as $\text{round}(g_{i,t})$ using eq. 3.3. Assign each birth an individual effect h_i from eqn SK, SU, or UU. To allow for comparability with the SK model, new individuals added in the SU model have their individual effects drawn conditionally on individuals present at the site. This means that individuals belong to the same joint distribution. To allow comparability across different levels of E in the UU model, which is blind to landscape structure, the constant c_k is $trace(\tilde{\mathbf{C}})(En_{k,t})^{-1}$, because $\tilde{\mathbf{C}}$ scales with $En_{k,t}$.

    (b) For SU, update the individual covariance matrix $\tilde{\mathbf{C}}_{k,t}$.

    (c) Evaluate survival (eq. 3.4) and accumulate dispersers for redistribution (eq. 3.5).

    (d) Update local density, including dispersers, using eq. 3.6.

6. Repeat this simulation and accumulate metrics, including final values $\bar{n}_{s,T} = K^{-1} \sum_k n_{sk,T}$, richness $= \sum_k I(n_{sk,T} > 0)$ (Fig. 24b), diversity $= -\sum_s \bar{n}_{s,T} \log(\bar{n}_{s,T})$ (Fig. 24a), site sorting $= Cor(\mathbf{K}, n_{sk,T})$, and species sorting $= Cor(\mathbf{C}, Cov(n_{sk,T}))$. Site sorting compares environment-species performance in $\mathbf{K} = \mathbf{ES}$ with their abundance in simulation (Fig. 24b). Species sorting compares the species covariance obtained from environmental responses with species covariance in simulation (Fig. 24c).

Table 15: Parameter values for Fig. 24 of the main text.

Parameter	**Dashed lines**	**Solid lines**
sites (K)	50	500
species (S)	100	500
percent dispersal (q)	10%	5%
local site capacity ± SD (C, z)	200 ± 100	200 ± 100
SD's (σ, τ)	0.03	0.03

Explanation: higher dimensionality leads to higher diagonal concentration in a correlation matrix

In Chapter 3, we show by example that increasing the number of dimensions (E) leads to a higher concentration of the correlation matrix on the diagonal. Here is an analytical explanation (by Isabelle Maréchaux) of this phenomenon. In other words, we here explain mathematically why the diagonal elements of the C matrix become more positive in comparison to off-diagonal elements when increasing E.
Considering the matrix:

$$C = S'V_ES$$

Where S is a species response matrix whose elements are denoted $\beta_{l,i}$, with $1 \leq l \leq E$ and $1 \leq i \leq S$, and V_E is the covariance matrix of the environment whose elements are denoted $V_{l,m}$ with $1 \leq l, m \leq E$ (see Eq. SU of Chapter 3)
then, by definition, for any $1 \leq i, j \leq S$:

$$C_{i,j} = \sum_{l=1}^{E} \sum_{m=l}^{E} V_{l,m} \times (\beta_{m,i}\beta_{l,j} + \beta_{l,i}\beta_{m,j})$$

Which we can write in two terms as follows:

$$C_{i,j} = \sum_{l=1}^{E} 2 \times V_{l,l} \times \beta_{l,i}\beta_{l,j} + \sum_{l=1}^{E-1} \sum_{m=l+1}^{E} V_{l,m} \times (\beta_{m,i}\beta_{l,j} + \beta_{l,i}\beta_{m,j})$$

where the first term has E elements, while the second has $E(E-1)$ elements.
When i = j (diagonal elements), this leads to:

$$C_{i,i} = \sum_{l=1}^{E} 2 \times V_{l,l} \times \beta_{m,i}\beta_{l,i} + \sum_{l=1}^{E-1} \sum_{m=l+1}^{E} 2 \times V_{l,m} \times \beta_{m,i}\beta_{l,i}$$

So when moving from $C_{i,j}$ with $i \neq j$ (off-diagonal elements) to $C_{i,i}$, we “exchange” E terms (the first sum) that are distributed among positive and negative values, with E terms that are all positive ($\beta_{l,i}^2$) and that are multiplied by the positive diagonal terms of the V_E matrix .
More concretely, if we assume that the $\beta_{l,i} \sim \mathcal{N}(0,1)$ for any $1 \leq l \leq E$ and $1 \leq i \leq S$,
then $E(\beta_{l,i}\beta_{m,j}) = E(\beta_{l,i})E(\beta_{m,j}) = 0$
and $V(\beta_{l,i}\beta_{m,j}) = V(\beta_{l,i})E(\beta_{m,j}) + V(\beta_{l,i})E(\beta_{m,j})^2 + V(\beta_{m,j})E(\beta_{l,i})^2 = 1$
while $E(\beta_{l,i}^2) = V(\beta_{l,i}) = 1$ and $V(\beta_{l,i}^2) = 2$.
Then if, additionally, we assume that all $V_{l,l} = 1$, we can say that the first term in $C_{i,i}$ has a mean of $2E$ (and a variance of $8E$, while staying positive), while the first term in $C_{i,j}$ with $i \neq j$ has a mean of 0 (and a variance of $4E$). On the contrary, the second terms in both $C_{i,j}$ with $i \neq j$ and $C_{i,i}$ should follow the same distribution.

Glossary

Adaptation Inherited characteristics that give an organism the ability to survive and reproduce in a particular environment (Reece et al. 2011).

Allelopathy Biological phenomenon by which an organism produces one or more biochemicals that influence the growth, survival, and reproduction of other organisms (Mougi 2013).

Attributes (species' or individuals') In this thesis, the term "attributes" refers to a broad definition of the term "trait" (see below) which encompasses all characteristics of a species or an individual, from phenotypic characters (*e.g.* colour) to functional traits (see definitions below) to demographic rates (growth, recruitment and mortality).

Coexistence Capacity of different species to co-occur, permanently (stable coexistence) or transiently (unstable coexistence) (Chesson 2000b). Coexistence theory focuses on explaining how competitors can coexist.

Community Co-occurring assemblages of trophically similar species (Hubbell 2005). Organisms that co-occur within a local place and time (Vellend 2010; Violle et al. 2012).

Community ecology Field of ecology that studies patterns in the composition and diversity of species (Vellend 2010); Field of ecology that aims at documenting and predicting the structure and dynamics of assemblages of organisms that co-occur within a local place and time (Vellend 2010; Violle et al. 2012).

Community structure Characteristics of a community like the number of species, species abundances, and relationships between species (like food webs).

Competitive exclusion Elimination of a species from a community due to competition for limited resources with other species that performed better. Refer to section I.2.a. for a more detailed explanation.

Conspecifics Individuals belonging to the same species.

Developmental noise Variability that arises during development from stochasticity in cellular and molecular processes when genotype and environment are fixed. It contributes to phenotypic variation (Kiskowski et al. 2019).

Epigenetic variation Interactions among molecular processes that alter gene expression and function without changing the underlying DNA sequence (Westerband et al. 2021).

Equilibrium Ecological **equilibria**, popularised as "the balance of nature", are states of ecological systems where a small deviation can be corrected by negative feedbacks, like a Newtonian equilibrium in physics. This is an assumption implying that nature is ordered and harmonious, and that deviations from an equilibrium state are caused by external perturbations, most often human (Maris et al. 2018).

Evolution Changes in the genetic composition of a population from generation to generation (Reece et al. 2011)

Facilitation Species interaction where one species has a positive impact on the fitness of another species.

Fitness (or performance) Quantitative representation of individual's reproductive success; relative contribution of an individual to the gene pool of the next generation (Reece et al. 2011). It can be approached by its three components, growth, reproduction and survival (which are thus performance proxies).

Food web Map that describes which kinds of organisms in a community eat which other kinds (Pimm et al. 1991).

Gap dynamics Process by which one or a few trees die, leaving a gap in the forest canopy that is then filled by other trees (Brokaw and Busing 2000).

Genetic drift Process in which random events cause unpredictable fluctuations in allelic frequencies from one generation to the next. The effects of genetic drift are most pronounced in small populations ((Reece et al. 2011)

Genotypic variation Variation between individuals due to differences in their genotype (number and structure of chromosomes and genes).

Heterospecifics Individuals belonging to different species.

Limited dispersal In ecology, dispersal is any movement of individuals or propagules with potential consequences for gene flow across space. Dispersal movement comprises three stages: (a) departure (or emigration), (b) a vagrant stage, and (c) settling (or immigration). Dispersal can be global or limited in space (Ronce 2007).

Limiting factor Environmental variable, in limited supply, that has the capacity to constrain a population's size. For instance, a limiting resource is a resource which can be experimentally shown to be limiting the reproduction of at least one member of the community (Tilman 1982). The law of minimum states that the scarcest resource drives growth.

Microbial mediation Role of microorganisms in shaping plant interactions and communities (Hodge and Fitter 2013).

Niche (ecological niche) Singular "way of life" of a species. Refer to section I.2.a. for a more detailed explanation.

Ontogeny Whole-plant ontogeny is the development of plants through stages, from seedling to juvenile/sapling, mature and finally senescent stage (Barton and Boege 2017).

Phenotypic plasticity Range of phenotypes (*i.e.* observable characteristics of an organism) that a single genotype can express as a function of its environment (Nicotra et al. 2010).

Population Localized group of individuals of the same biological species that live in the same area, reproduce and produce fertile offsprings (Reece et al. 2011).

Population ecology Field that studies of the mechanisms responsible for changes in the distribution and abundance of individuals over space and time (Koons 2021).

Population dynamics Study of the fluctuations in time and space of the demography of populations.

Random mutation Random modification of the DNA sequence of an organism (or RNA sequence of a virus), that can be heritable, and can give selective advantages or disadvantages or be selectively neutral.

Speciation Process leading to the apparition of new species, for instance through geographical barriers preventing gene flow.

Taxonomy Science that explores, describes, names, and classifies all organisms (Rouhan and Gaudeul 2014).

Trade-off (ecological trade-off) Fact that, due to costs, a species cannot be good in every situation. Refer to section I.2.a. for a more detailed explanation.

Trait A trait is any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization. Functional trait indirectly impacts fitness via its effect on performance traits (*e.g.* one of the fitness components: growth, reproduction, survival). Demographic traits are often used at the population level to describe the rates of birth, death, immigration and emigration, but *sensu lato* they can describe the performance traits of an individual. Life-history traits can also be performance traits, or describe the processes that explain performance traits (*e.g.* timing of germination). There are several classifications of traits. For instance, response traits describe the response of an individual to environmental changes while an effect trait describes the effect of an individual on ecosystem functioning. (Violle et al. 2007)

Trophic level Set of species which consume the same resources in a community. This concept comes from a linear view of trophic relationships (*i.e.* the food chains) but as complexity is acknowledged (*i.e.* with food webs), the definition of a trophic level becomes challenging and its usefulness questioned. However, this issue is minor for green plants which are mostly in the same trophic level since they have the same basic requirements (light, water, CO_2, soil nutrients) as primary producers.

Abstract / Résumé

Résumé Le fait que des espèces coexistent alors qu'elles sont en compétition pour les mêmes ressources – par exemple les espèces d'arbres dans les forêts tropicales – reste une question fondamentale en écologie des communautés. Alors que cette question a traditionnellement été abordée avec des caractéristiques moyennes par espèce, la variabilité intraspécifique (VI) a récemment connu un regain d'intérêt, notamment en raison de la mise en évidence de la part importante de la variabilité totale que représente la VI dans une communauté. Par la suite, la VI a été principalement représentée dans les études de modélisation par des tirages aléatoires indépendants dans une distribution de probabilité. Cela implique l'hypothèse implicite que la VI est un bruit sans structure spatio-temporelle, qui atténue les différences entre les espèces. Cette hypothèse a mené à des résultats contradictoires concernant les conséquences de la VI sur la coexistence des espèces. L'objectif principal de cette thèse est de fournir des éléments de réflexion sur la nature et la structure de la VI, sur la façon dont elle est prise en compte en écologie, en particulier dans les modèles de dynamique des communautés, et sur ses conséquences pour la coexistence des espèces. Dans un premier chapitre, nous illustrons comment la VI observée peut provenir de variations environnementales dans de nombreuses dimensions imparfaitement caractérisées, et non pas nécessairement de variations génétiques entre individus d'une même espèce. Cela peut conduire à une structure spatio-temporelle de la VI si ces facteurs environnementaux sont structurés, et ne mène pas nécessairement à une superposition des niches écologiques des espèces. Nous combinons des preuves empiriques que la VI peut être due à des facteurs non génétiques, que la VI est structurée dans l'espace, et que malgré une forte VI observée, les performances des espèces restent différentes. Ce type de VI observée, qui a une structure spatio-temporelle particulière, n'est donc pas un mécanisme de coexistence en soi mais plutôt la signature de la réponse des espèces à un environnement multidimensionnel qui varie dans l'espace et le temps. Nous suggérons que ce type de VI est rarement pris en compte de manière adéquate dans les modèles de dynamique des communautés. Dans un deuxième chapitre, à l'aide d'un modèle simple de dynamique des communautés, nous testons l'effet de la manière dont la VI est introduite dans les modèles sur la composition des communautés simulées, dont le nombre d'espèces coexistantes. Nous montrons que les distributions aléatoires simples ne constituent pas une bonne approximation de la VI dans les systèmes présentant une structure environnementale. Dans un troisième et dernier chapitre, en utilisant également une approche de simulation, nous montrons que les différences entre espèces et la variation de nombreuses dimensions environnementales conduisent conjointement à un niveau élevé de coexistence et se traduisent par une structure particulière des corrélations de performance individuelle où les individus conspécifiques ont des performances plus similaires que les hétérospécifiques. Nous montrons ensuite comment l'introduction de cette VI structurée dans les modèles permet la coexistence d'un nombre élevé d'espèces grâce à un partitionnement de niche à haute dimension, même si les causes de cette structure sont inconnues et ne sont pas inclues dans le modèle. En définitive, nous espérons amener une nouvelle façon de considérer et de représenter la VI en écologie des communautés. Nous apportons des perspectives de tests plus poussés sur la structure de la VI et pour l'intégration de la VI dans les modèles de dynamique des communautés.

Abstract The fact that many species are able to coexist while competing for the same resources – for instance tree species in tropical forests – remains a major conundrum in community ecology. While it has been traditionally approached using species mean characteristics, intraspecific variability (IV) has recently gained renewed interest, notably with evidences of the large amount of variability that IV represents in a community. Since then, IV has been predominantly represented in modeling studies through independent random draws in a probability distribution. In doing so, IV is implicitly assumed to be a noise with no structure in space or time that blurs the differences between species. This assumption led to inconsistent results about consequences of IV on species coexistence. The main objective of this PhD is to provide insights into the nature and structure of IV, on the way it is considered in ecology - particularly in community dynamics models - and on its consequences for species coexistence. In a first chapter, we first illustrate how observed IV can arise from environmental variations in many dimensions that are imperfectly characterised, and not necessarily from genetic variations between individuals of the same species. This can lead to spatio-temporal structure in IV if these environmental drivers are structured, and does not necessarily make species niches overlap. We then combine empirical evidence that IV can be due to non-genetic factors, that IV is structured in space, and that although a high IV observed, species performances are not similar. This type of observed IV, which is spatio-temporally structured, is thus not a coexistence mechanism per se but is the signature of the response of species to a multidimensional environment that varies in space and time. We argue that this type of IV is often not well accounted for in community dynamics models. In a second chapter, using a simple community dynamics model, we test the effect of the way IV is introduced on the composition of the simulated communities, including the number of coexisting species. We show that simple random distributions are not a good proxy for IV in systems with environmental structure. In a third and final chapter, using a simulation approach as well, we show that species differences and variation in many environmental dimensions together lead to a high number of coexisting species, and translates into a particular structure of individual performance correlations where conspecific individuals perform more similarly than heterospecifics. We then show how introducing this structured IV in models enables the coexistence of a high number of species thanks to high-dimensional niche partitioning, even though the drivers of this structure remain unknown and are not included in the model. Overall, we hope to trigger a renewed way to consider and represent IV in community ecology, and provide perspectives for additional tests on the structure of IV and for its integration in community dynamics models.