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**Estimation de biomasse en
forêt tropicale humide**

Propagation des incertitudes dans la modélisation de la
distribution spatiale de la biomasse en Guyane française

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Résumé

Les émissions de carbone d'origine humaine causent actuellement une modification des mécanismes climatiques mondiaux. Ces changements de climats sont dangereux pour les populations humaines. Des programmes internationaux sont mis en place pour tenter de réduire l'impact des activités humaines sur le climat. Dans le cadre du REDD+, il s'agit de réduire les émissions issues de l'impact humain sur les forêts. Cela requiert de mieux connaître les forêts et en particulier les forêts tropicales qui sont souvent situées dans des pays à forte croissance.

Dans cette thèse, nous nous intéressons au carbone stocké dans la biomasse vivante des forêts naturelles. Ce stock de carbone important à l'échelle du globe est assez mal connu. L'étude de la biomasse permet de quantifier l'impact des activités humaines sur la forêt et d'essayer de mieux comprendre son fonctionnement écologique. Les modèles développés au cours de la thèse sont appliqués à des données récoltées en Guyane française entre 1972 et 2011.

La Guyane française est une région située sur le plateau des Guyanes en Amérique du sud. Ce territoire est presque intégralement recouvert d'une forêt tropicale très préservée car l'activité humaine y est très faible. Dans le même temps, les organismes de recherche sont présents depuis longtemps en Guyane française et de nombreuses données sont disponibles. C'est donc un lieu de choix pour étudier les forêts tropicales naturelles.

Ce manuscrit de thèse prend la forme dite "sur article", c'est à dire que les différents chapitres qui le composent sont des articles scientifiques publiés ou en cours de publication. Ces chapitres sont précédés d'un chapitre introductif et suivis d'un chapitre de synthèse :

- Le premier chapitre introduit la problématique de l'estimation de la biomasse des forêts tropicales dans le cadre des changements climatiques globaux.
- Dans le second chapitre, nous comparons différentes méthodes d'inventaires forestiers : certaines méthodes d'inventaires sont-elles meilleures que d'autres pour estimer la biomasse d'une région ? Cet article a été accepté pour publication dans *Biotropica*.
- Dans le troisième chapitre, nous définissons les modèles permettant à l'estimation de la biomasse des parcelles inventoriées. Nous analysons ces modèles : quelles sont les sources d'incertitude des estimations de biomasse ? Cet article a été accepté pour publication dans *Methods in Ecology and Evolution*.
- Dans le quatrième chapitre, nous étudions la relation entre le diamètre et la hauteur des arbres : Comment prédire les hauteurs des arbres pour améliorer les prédictions de biomasse ? Ce manuscrit sera soumis pour publication dans une revue scientifique au cours du mois de novembre.
- Dans le cinquième chapitre, nous utilisons les modèles développés précédemment pour estimer la biomasse de nombreuses parcelles inventoriées en Guyane française. Grâce à ces parcelles, nous pouvons modéliser la variabilité spatiale de la biomasse en lien avec des variables décrivant l'environnement (climat, géologie, relief, ...). Nous produisons ainsi une carte de la biomasse de la Guyane française associée à une carte de l'incertitude associée à cette biomasse. Nous envisageons de soumettre ce manuscrit pour

publication dans une revue scientifique au mois de décembre.

- Dans le dernier chapitre, après une synthèse des principaux résultats, nous proposons des pistes de développements futures.

En annexe est présenté un article auquel j'ai participé au début de ma thèse (analyse des données). Cet article n'est pas inclut en tant que chapitre de ma thèse, cependant les idées et les méthodes qui y sont développées ont beaucoup inspiré mon travail.

Chapitre 1

Introduction

1.1 Le carbone terrestre

1.1.1 Le cycle du carbone

Le carbone terrestre est contenu sous différentes formes dans quatre grands compartiments (Sabine *et al.*, 2004) :

- La lithosphère contient du carbone dans ses roches carbonées et carbonatées (30 000 000 Gt).
- L’hydrosphère contient du carbone sous forme dissoute (38 000 Gt) et dans les organismes marins (3 Gt).
- La biosphère contient 2 300 Gt de carbone sous forme de matière vivante (biomasse), de matière morte (nécromasse), et dans les sols.
- L’atmosphère contient 700 Gt de carbone sous forme de CO_2 .

Actuellement, la lithosphère échange peu de carbone de façon naturelle avec les autres compartiments. Les roches calcaires ou carbonatées sont formées par sédimentation. L’émission de CO_2 dans l’atmosphère lors de l’utilisation de combustibles fossiles dans les activités humaines est actuellement le flux principal

qui concerne ce stock.

L'hydrosphère et la biosphère sont à l'équilibre par la dissolution du CO_2 atmosphérique dans les eaux de surface océaniques. Le CO_2 dissout est en partie stocké par la biosphère marine.

Enfin, la biosphère terrestre capte du carbone dans l'atmosphère lors de la photosynthèse et en rejette lors des réactions de respiration. Le carbone de la biosphère est presque entièrement contenu dans les écosystèmes forestiers.

Dans le cycle du carbone, la biosphère a un rôle particulier. C'est un compartiment qui est directement au contact des activités humaines. Il est possible d'agir sur ce compartiment. Le changement d'usage des terres fait diminuer son stock de carbone (Houghton *et al.*, 2001). Planter de nouvelles forêts ou protéger les forêts existantes peut le faire augmenter (Pan *et al.*, 2011).

1.1.2 Carbone et réchauffement climatique

En 2007, le Groupe d'Experts Intergouvernemental sur l'Evolution du Climat (GIEC, en anglais : International Panel on Climate Change (IPCC)) publie son quatrième rapport (Solomon *et al.*, 2007). Il y est clairement établi que l'augmentation de température observée depuis 1950 est d'origine anthropique. Les activités humaines qui émettent des gaz à effets de serre (GES) sont la première cause du réchauffement climatique. Parmi les GES, le CO_2 a le rôle le plus important (figure 1.1.1).

Dans ce même rapport, le GIEC détaille en cinq points les risques majeurs encourus par les populations humaines lors du réchauffement de la planète :

- La destruction de systèmes rares et déjà menacés, tels que les écosystèmes polaires, les régions montagneuses, ou les récifs coralliens.

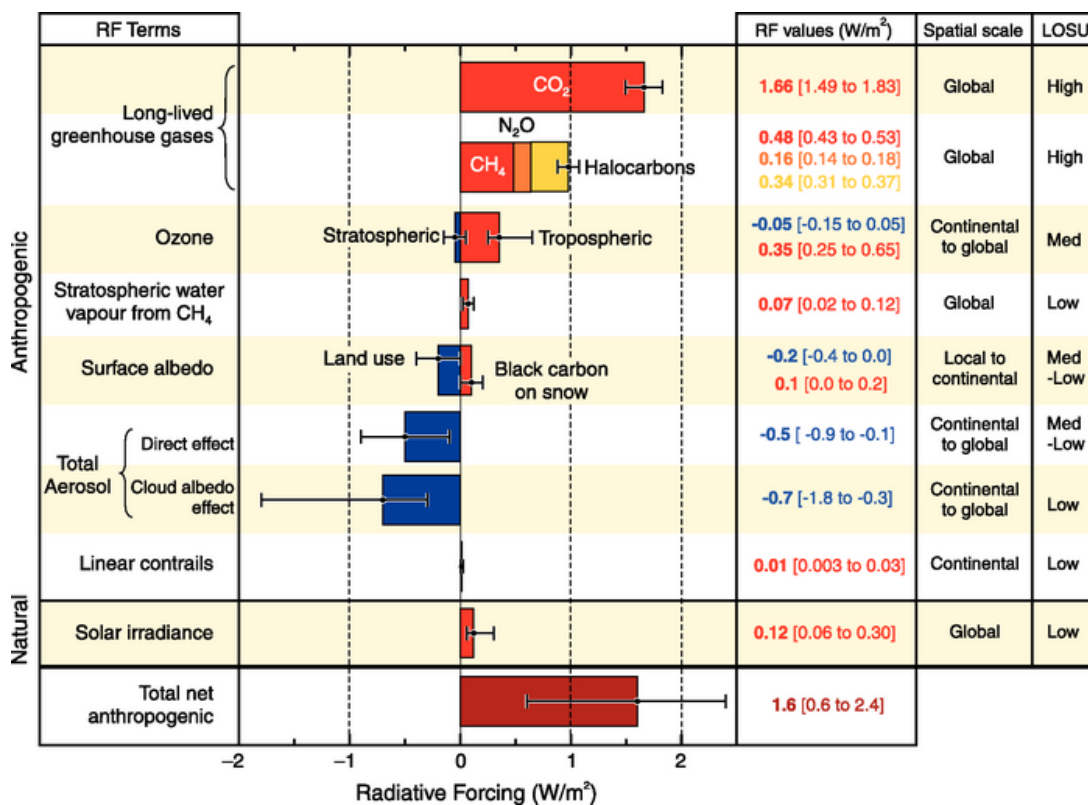


FIGURE 1.1.1 – Forçage radiatif (RF) de différents gaz à effet de serre et autres variables climatiques importants, leur échelle spatiale d'application, et leur niveau de documentation scientifique (LOSU). IPCC, Climate Change 2007 : Synthesis Report.

- L’augmentation de la fréquence des épisodes climatiques extrêmes (sécheresses, vagues de chaleur, inondations). Ces événements pourraient aussi se produire dans des régions où ils sont inconnus, frappant ainsi des populations non préparées.
- La déstabilisation de populations déjà affaiblies. Les pays les moins développés sont plus exposés aux effets du changement climatique. Dans tous les pays, les individus les plus fragiles (pauvres, très jeunes, très âgés) sont particulièrement exposés.
- La déstabilisation d’économies régionales, en particulier agricoles, basées sur un produit devenu inadapté aux nouvelles conditions climatiques locales.
- Des événements affectant l’ensemble de la planète tels que l’augmentation du niveau de la mer ou la réorganisation de la circulation océanique.

Par ailleurs, le Programme des Nations Unies pour l’Environnement (PNUE) souligne l’augmentation du risque de conflits. Les modifications climatiques seraient susceptibles de provoquer des migrations de populations et des guerres pour des ressources naturelles (eau, terres favorables à l’agriculture). Le PNUE s’attend aussi à des tensions déséquilibrées entre pays riches et pauvres pour l’accès aux ressources.

1.1.3 Les enjeux actuels

Face à ces dangers, la communauté internationale réagit. En 1972 a eu lieu la conférence des Nations Unies sur l’environnement (conférence de Stockholm). C’est lors de cette conférence que le PNUE a été créé. Pour la première fois, les questions écologiques sont au cœur de débats internationaux. Les pays participants se sont engagés à se revoir tous les dix ans pour faire le point sur l’état

environnemental de la Terre.

En 1992, lors de la conférence de Rio, les participants s'accordent sur la nécessité de stabiliser les concentrations atmosphériques en GES. L'objectif est de limiter la brutalité des changements pour que les écosystèmes aient le temps de s'adapter. La Convention-cadre des Nations Unies sur les changements climatiques (CCNUCC) crée une structure juridique permettant la négociation de protocoles contraignants sur le plan juridique.

En 1997, les 141 nations signataires du protocole de Kyoto s'engagent à réduire de 5,2 % leurs émissions de six GES entre 2008 et 2012 par rapport aux niveaux de 1990. Les pays en développement économique n'ont pas d'engagements dans ce protocole et les Etats-Unis, alors principal pays émetteur de carbone, ne sont pas signataires.

De manière pratique, cet accord pose les bases d'un marché du carbone. Les états qui dépassent les quotas fixés par les accords peuvent acheter des "crédits carbone" aux états qui ne dépassent pas leurs quotas d'émissions. Ces crédits permettent d'émettre plus de GES. L'objectif est de motiver les états à limiter leurs émissions de GES en donnant un coût financier à ces émissions.

Les accords de Copenhague, signés en 2009, devaient être une renégociation des accords de Kyoto. Cependant, aucun engagement quantitatif contraignant n'a été pris pour l'après 2012 (fin du protocole de Kyoto). Cependant, les 112 nations participantes se sont entendues pour tenter de limiter à 2°C la hausse de température par rapport à l'ère préindustrielle (1850).

Lors de la Conférence des Nations unies sur le développement durable tenu en 2012 à Rio, le PNUE a été renforcé dans son rôle de gestionnaire international des questions environnementales.

1.1.4 Les forêts, une préoccupation majeure

Dans le cadre des accords internationaux sur la limitation des émissions de GES et de l'augmentation de la température, le cas des forêts et en particulier des forêts tropicales est un point important. Comme nous l'avons vu, ce stock de carbone est celui sur lequel il est le plus facile d'agir. Cependant, les forêts tropicales sont principalement situées dans des pays au développement rapide (bassin de l'Amazonie, bassin du Congo, Asie du Sud-est). Ces pays qui connaissent une forte croissance économique et démographique ne souhaitent pas voir leur développement bridé par des protections trop strictes de leurs ressources naturelles.

Lors de la seizième Conférence des parties à la convention sur les changements climatiques de Cancún (2010), le programme REDD+ a été adopté. REDD+ signifie "Reducing Emissions from Deforestation and Forest Degradation" (Réduction des Emissions venant de la Déforestation et de la Dégradation des forêts). Le "+" indique l'intégration dans le programme de notions de protection des forêts, d'augmentation des stocks de carbone forestiers, et de gestion durable des forêts. Le programme REDD+ doit permettre de développer une "économie verte" en rendant les investissements qui ont des effets positifs sur le climat plus séduisants (Sukhdev *et al.*, 2012).

Le programme REDD+ doit aussi permettre aux états qui protègent leurs forêts d'accéder au marché du carbone. L'évitement de la destruction ou de la dégradation de la forêt génère un "crédit carbone" et la vente de ce crédit sur le marché du carbone permet de compenser la perte économique due à la protection de la forêt. Dans ce cadre, le REDD+ met en place des conventions entre états définissant et validant les efforts de protection.

Il est alors nécessaire de pouvoir chiffrer les quantités de carbone contenues dans les forêts.



FIGURE 1.2.2 – Forêts comprises entre les deux tropiques. La définition de la FAO désigne comme "tropicale" une forêt dans laquelle la température mensuelle moyenne est toujours supérieure à 18 °C (FAO, 2000).

1.2 Les forêts tropicales

Les forêts tropicales recouvrent une surface de 1949.10^6 ha, c'est à dire 50% de la surface forestière mondiale. Elles sont situées dans la zone intertropicale sur trois continents : L'Amérique du Sud, l'Afrique, et l'Asie du Sud-est (figure 1.2.2). Ainsi réparties, les forêts tropicales sont soumises à des régimes climatiques variés (Malhi *et al.*, 2004).

1.2.1 Un stock de carbone important

Les forêts tropicales renferment environ 40% du carbone stocké dans la végétation mondiale (Houghton *et al.*, 2001; Malhi *et al.*, 2006). Cependant, l'incertitude sur ces estimations est très importante (Gibbs *et al.*, 2007; Pan *et al.*, 2011).

En tant qu'écosystème, une forêt contient du carbone dans plusieurs compartiments. A l'échelle mondiale, le carbone se répartit de la façon suivante : sol (45%), nécromasse (biomasse morte, 11%), et biomasse vivante (aérienne et souterraine, 44%) (FAO, 2000). Ces proportions sont susceptibles de varier grandement d'un biome à l'autre. Parmi ces compartiments, la biomasse aérienne vivante est la plus étudiée car c'est la plus accessible. Les autres compartiments

peuvent aussi stocker des quantités de carbone importantes et sont affectés par la destruction de la forêt, de manière moins immédiate. Cependant, la biomasse aérienne vivante reste la variable de référence pour décrire le carbone stocké dans les forêts.

Dans notre étude, nous appelons "biomasse" **la masse fraîche aérienne vivante des végétaux ligneux d'un diamètre supérieur à 10 cm.**

La biomasse est la masse de la matière vivante. Cette masse peut être convertie en masse de carbone pur. Il est généralement acquis, d'après la composition chimique du bois, que la masse d'atomes de carbone est la moitié de la biomasse. Cette relation varie légèrement selon les essences de bois ou selon l'environnement. Cette relation est basée sur des données très limitées et devrait être plus étudiée de manière à améliorer la qualité des conversions de biomasses en masses de carbone (Lamloom & Savidge, 2003; Martin & Thomas, 2011). La conversion de la biomasse fraîche en biomasse sèche puis en masse de carbone ne fait pas partie du périmètre de notre étude.

La biomasse souterraine et la biomasse morte peuvent être estimées à partir de la biomasse aérienne. Des modèles, sous forme de facteurs de correction, ont été calibrés dans différentes régions. Par exemple, pour les forêts tropicales d'Amérique du Sud, la biomasse souterraine serait égale à $0.20 * Biomasse$ et la nécromasse à $0.06 * Biomasse$ (FAO, 2010).

De la même façon, la biomasse contenue dans les plus petits arbres et dans les autres plantes (lianes, palmiers) ne devrait pas être négligée. Ces plantes sont souvent absentes des inventaires et leurs biomasses ont été étudiées localement (Brown *et al.*, 1989). Des modèles existent pour calculer spécifiquement la biomasse des lianes (Gehring *et al.*, 2004) et des petits arbres (Hughes *et al.*, 1999).

Ces limitations dans la définition de la biomasse par rapport à la *vraie biomasse totale* sont plus ou moins gênantes selon les faciès forestiers. Dans un peuplement dominé par des grands arbres, les biais sont assez faibles (Baraloto *et al.*, 2011). Par contre, dans des forêts dominées par des arbres de faibles diamètres, des lianes, ou des palmiers, cette définition ne reflète pas la réalité du stock de carbone.

Malgré les limitations que cela semble impliquer, travailler sur la biomasse des plantes ligneuses au-delà d'une certaine taille respecte les bonnes pratiques définies par la FAO et le PNUE dans le cadre de l'IPCC (Eggleston, 2006). Ces pratiques doivent être uniformisées de façon à ce que les valeurs puissent être comparables entre régions, pays, continents.

1.2.2 Un stock de carbone dynamique

Si le carbone stocké dans les forêts tropicales suscite tant d'intérêt, c'est parce qu'il est susceptible d'être émis dans l'atmosphère. La déforestation et le changement d'usage des terres en zone tropicale sont responsables de 15 à 20 % des émissions de GES mondiales (Malhi & Grace, 2000; Fearnside & Laurance, 2004; Houghton, 2005).

A l'inverse, si des forêts sont plantées ou se régénèrent spontanément, c'est autant de carbone qui est séquestré dans le nouveau peuplement forestier. Cependant, la résilience des forêts tropicales est assez faible (Aide *et al.*, 2000). Lors de la régénération naturelle, le stock de carbone de la forêt ne revient pas à son niveau antérieur en quelques décennies (Foody *et al.*, 1996).

Sans destruction ni régénération (c'est à dire sans modification de surface occupée), la forêt tropicale peut subir des changements qui affectent sa biomasse. Par exemple, une augmentation de la mortalité diminue la biomasse vivante et

augmente la nécromasse dont le carbone est relargué dans l'atmosphère plus ou moins rapidement (Hérault *et al.*, 2010). Les changements climatiques actuels sont particulièrement susceptibles d'augmenter la mortalité des arbres, en particulier lors des sécheresses (Phillips *et al.*, 2009; Allen *et al.*, 2010).

Sous l'influence de nouveaux paramètres environnementaux, la biomasse de la forêt pourrait aussi augmenter. L'augmentation de la concentration en CO_2 dans l'atmosphère est susceptible de stimuler l'activité photosynthétique des arbres et peut ainsi créer un flux net de carbone entrant (Phillips *et al.*, 1998; Malhi & Grace, 2000; Pan *et al.*, 2011). Cet effet de la fertilisation atmosphérique est sujet à controverse dans les forêts boréales (Körner, 2004; Hickler *et al.*, 2008) comme dans les forêts tropicales (Clark, 2007; Lewis *et al.*, 2009; Clark *et al.*, 2010).

1.3 Problématique

Les problématiques liées au stockage de carbone dans les forêts tropicales requièrent l'estimation de ce stock. Que ce soit dans le cadre du REDD+ ou du cycle du carbone (échange avec l'atmosphère), l'estimation du stock de biomasse doit être associée à une incertitude. Par exemple, une estimation de la biomasse d'une forêt peut se traduire par une émission de GES lors de l'exploitation de cette forêt. Cette incertitude sur les émissions de GES influe sur l'incertitude associée aux prévisions d'évolutions climatiques. En ce qui concerne les variations spatiales et temporelles, la quantification des incertitudes permet de savoir si les différences observées sont "significatives". Par exemple, des différences de biomasse de l'ordre de 5% sont peut-être à relativiser si l'incertitude sur les valeurs est de 20%.

La biomasse d'une parcelle de forêt ne peut être mesurée directement que d'une seule façon : en abattant les arbres et en mesurant leurs masses. Cette

méthode de mesure a une très grande précision mais est destructive. Par contre, d'autres variables peuvent être récoltées de façon non destructive pour caractériser les arbres de la parcelle. Des modèles relient ensuite ces variables à la biomasse. Selon la façon dont la parcelle a été inventoriée, différents modèles peuvent être nécessaires, apportant chacun leur incertitude.

Dans un second temps, il faut prédire la biomasse en dehors des parcelles inventoriées. Ces parcelles servent alors de données de calibration pour des modèles reliant la biomasse de la parcelle à des variables décrivant la forêt ou le paysage forestier. Ces variables peuvent caractériser la forêt directement (images aériennes par exemple) ou indirectement (caractérisation de l'environnement par exemple).

L'estimation de la biomasse d'une forêt nécessite l'usage de plusieurs modèles successifs. Pour quantifier l'incertitude associée à une estimation de biomasse, l'incertitude apportée par chaque modèle doit être propagée jusqu'à l'estimation finale. L'objectif de la thèse est de développer des modèles et des méthodes permettant d'estimer la biomasse d'une forêt tropicale ainsi que son incertitude. Pour atteindre cet objectif, nous allons :

- Quantifier l'incertitude associée à l'estimation de la biomasse d'une parcelle inventoriée et identifier les sources de cette incertitude.
- Proposer des modèles adaptés permettant de réduire cette incertitude.
- Mettre en œuvre les méthodes proposées pour estimer la biomasse d'une région : la Guyane française.

1.4 Estimations de biomasse

Les mesures de biomasse ne pouvant pas être destructives à grande échelle, il est nécessaire d'utiliser des méthodes non destructives. Les méthodes non des-

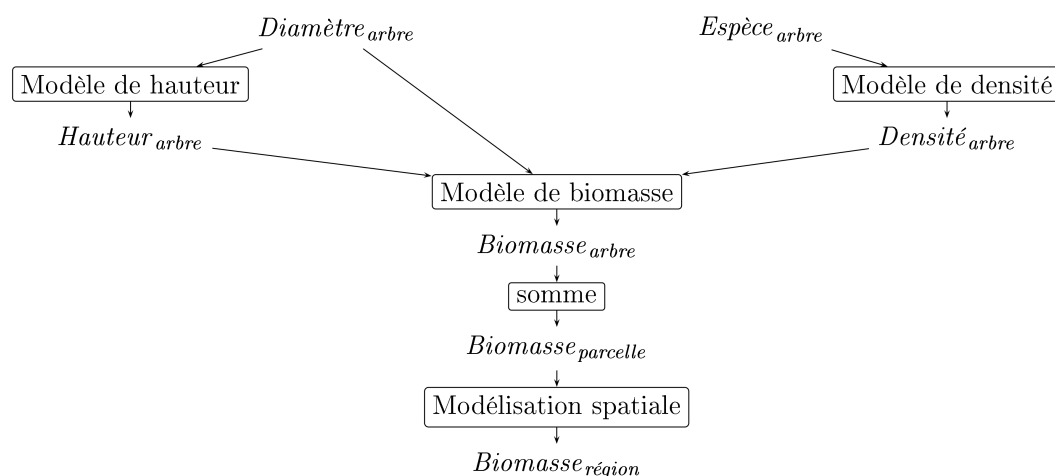


FIGURE 1.4.3 – Processus d’estimation de la biomasse d’une région et schéma de propagation des incertitudes

tructives sont indirectes et se basent sur des modèles reliant les caractéristiques de la forêt à sa biomasse. Dans un premier temps, un modèle à l’échelle de l’arbre permet de connaître la biomasse de parcelles forestières inventoriées. Dans un second temps, un modèle à l’échelle de la parcelle forestière permet de relier la biomasse de la forêt à des variables la décrivant. Cette succession de modèles est représenté sur la figure 1.4.3.

Les variables mesurées pour chaque arbre d’un inventaire forestier varient d’un inventaire à l’autre. Dans un souci d’uniformisation internationale des pratiques, la FAO et l’IPCC ont émis des recommandations (Brown, 1997; Eggleston, 2006) régulièrement mises à jour.

1.4.1 Un modèle à l’échelle de l’arbre

Les vraies mesures de biomasses impliquent de peser des arbres après les avoir abattus. Ces mesures sont destructives et très contraignantes (Araujo *et al.*,

1999b; Nogueira *et al.*, 2008), les vraies données de biomasse sont donc plutôt rares. En 2005, ces données ont été rassemblées à l'échelle mondiale (Amérique du sud, Asie, Océanie) (Chave *et al.*, 2005) et un modèle de biomasse pantropical a été calibré. Actuellement, ce modèle est utilisé dans toutes les forêts tropicales du monde.

Du modèle mécaniste au modèle statistique

Le modèle se base sur la formule de calcul de la masse M d'un cylindre de diamètre D , de longueur H , et de densité WD (pour Wood Density, densité de bois en anglais) :

$$M = \pi * (D/2)^2 * H * WD$$

soit

$$\log(M) = \log(\pi) + \log(1/2) * \log(D) + \log(H) + \log(WD)$$

A partir de cette formule, un modèle est construit par l'ajout de coefficients permettant l'ajustement à la masse M_i d'un arbre au lieu d'un cylindre (figure figure 1.4.3). Un terme d'erreur ϵ_i rend compte de la différence de masse entre deux arbres de mensurations identiques :

$$\log(M_i) = \beta_0 + \beta_1 * \log(D_i) + \beta_2 * \log(H_i) + \beta_3 * \log(WD_i) + \epsilon_i$$

$$\epsilon_i \sim N(0, \sigma^2)$$

Ce modèle assez naturel n'a jamais été remis en cause et s'ajuste bien aux données. Certains auteurs suggèrent qu'il n'est pas nécessaire de conserver un coefficient par variable pour des raisons de parcimonie (critère d'Akaike) (Chave

et al., 2005). Nous avons préféré conserver un coefficient par variable pour avoir un modèle plus souple.

La biomasse d'un arbre est prédite grâce aux coefficients β du modèle. Dans la majorité des cas, un modèle de référence est utilisé, généralement celui publié par Chave *et al.* en 2005. Ce modèle est calibré sur une compilation de données tropicales. Dans de nombreuses régions, des études sont en cours pour valider ce modèle ou en développer un nouveau le cas échéant mais la relation semble très stable entre les différentes forêts tropicales (Vieilledent *et al.*, 2011).

Lors de l'utilisation d'un modèle pour prédire la masse des arbres d'un inventaire, il faut que les variables mesurées lors de l'inventaire soient mesurées de la même façon que pour les données de calibration. Il est donc primordial de décrire précisément comment le diamètre, la hauteur, et la densité de bois sont définis lors de la publication d'un tel modèle. Il est également impératif que les données de calibration soient représentatives des arbres de l'inventaire auquel le modèle est appliqué. Si les arbres ont été abattus de manière aléatoire, la proportion d'arbres creux ou endommagés sera réaliste et représentative du site. Si seuls des arbres sains sont abattus et pesés, l'application du modèle à un inventaire causera une surestimation de la biomasse. Cette surestimation peut être importante (Nogueira *et al.*, 2006).

Une attention profonde doit donc être portée à la définition des variables. la façon de mesurer la hauteur est assez universelle (distance entre le sol et l'élément le plus haut de l'arbre), de même que la façon de mesurer le diamètre (à hauteur de poitrine, au dessus des contreforts si nécessaire). En revanche, la façon de mesurer la densité du bois est sujette à plus de discussions (Williamson & Wiemann, 2010).

Des données manquantes

Les mesures de diamètre sont la base des inventaires forestiers utilisables pour des estimations de biomasse. Cette variable est toujours présente. Le diamètre est mesuré à hauteur de poitrine (en anglais, DBH : Diameter et Breast Height) et au-dessus des contreforts si nécessaire (Brown, 1997). La valeur de diamètre minimum est généralement de 10cm. Cette valeur limite est cohérente avec l'inventaire d'une forêt dominée par des grands arbres. La masse des plus petits arbres et des autres végétaux ne dépasse alors pas 3% de la biomasse totale (Tanner, 1980; Baraloto *et al.*, 2011; Keeling & Phillips, 2007). Cette limite de 10cm peut ne pas être adaptée dans des peuplements dominés par des tiges fines ou des plantes herbacées ; il convient alors de la diminuer (Brown, 1997).

En revanche, la hauteur des arbres, beaucoup plus contraignante à mesurer, ne l'est que rarement. La densité de bois, enfin, n'est jamais mesurée à l'échelle d'un inventaire.

Deux approches permettent de compenser l'absence de ces variables. La première approche consiste à calibrer des modèles sans hauteurs ou basés sur le diamètre uniquement (Pilli *et al.*, 2006). La seconde approche est de prédire les données manquantes de hauteurs et de densité de bois par des modèles. Il est même possible de mixer les deux approches (Chave *et al.*, 2005).

Nous pensons qu'il est préférable de garder toutes les variables dans le modèle (figure 1.4.3). Ainsi, toutes les informations peuvent être prises en compte. Si aucune information pertinente n'est disponible alors un modèle naïf peut être utilisé. De plus, de nombreux auteurs ont insisté sur l'importance de prendre en compte la densité de bois (Baker *et al.*, 2004) et la hauteur des arbres (Feldpausch *et al.*, 2011) lors des estimations de biomasse.

Modèle de densité de bois

La densité de bois est prédite à partir de l'espèce d'un arbre. Quand les arbres de l'inventaire ne sont pas identifiés ou quand l'espèce relevée n'a pas une densité connue, il faut une stratégie de remplacement de valeurs manquantes. Habituellement, cette stratégie est soit taxinomique (utilisation d'information taxinomique incomplète : Genre, Famille...) soit locale (utilisation des densités de bois des arbres proches) (Flores & Coomes, 2011). Le modèle naïf peut être une simple densité de bois moyenne à l'échelle régionale.

La densité de bois est une variable bien connue car elle est reliée aux propriétés mécaniques du bois. Cependant, il existe de nombreuses façons de la mesurer. Les différentes méthodes de mesure peuvent donner des valeur variables (Chave *et al.*, 2006; Williamson & Wiemann, 2010), nous pensons donc qu'il est important de prêter attention aux protocoles de mesure et de ne pas mélanger des mesures de densités de bois mesurées selon des protocoles différents.

Un des points importants est la définition de l'échantillon de bois sur lequel la densité est mesurée. Pour prédire la biomasse, la meilleure solution serait de tenir compte, de façon pondérée, de toutes les variations de densité des différents "matériaux" de l'arbre : les différents bois (aubier, duramen, branches...), les feuilles, les fruits... Cette définition est évidemment impossible à mettre en pratique. La mesure de densité de bois que l'on utilise n'est qu'une approximation proportionnelle à cette densité idéale hypothétique.

Le bois d'un arbre peut être échantillonné de multiples façons, de la plus complexe à la plus simple. Un échantillonnage complexe pourrait se faire sous forme de disques répartis le long du tronc. Ainsi, la mesure de densité de bois intègre la variabilité dans les trois dimensions : le plan horizontal (disques) et l'axe vertical (le long du tronc). Cet échantillonnage est destructif. Un échantillonnage de bois

plus simple consiste par exemple en de petites carottes de bois prélevées dans les troncs. Une telle méthode permet d'échantillonner de très nombreux arbres mais intègre moins la variabilité intra-individuelle de la densité de bois.

Une fois le protocole échantillonnage défini, la façon dont est séché le bois à son importance (durée, température). Certains auteurs proposent des équations pour relier les densités de bois issues de différents protocoles de séchage (Muller-Landau, 2004).

Pour conserver la même définition de la densité de bois tout au long de notre étude, nous avons utilisé un seul et unique jeu de données. Il s'agit des données récoltées lors du projet Bridge (Baraloto *et al.*, 2012). L'échantillon prélevé est un petit cylindre de bois de 6mm de long (Sarmiento *et al.*, 2011). Nous nous situons donc dans les prélèvements minimaux mais nous sommes très cohérents dans l'utilisation de cette variable : une seule base de donnée, données locales.

L'attribution d'une densité de bois à un arbre se fait généralement par simple lecture dans une base de donnée de la densité de bois moyenne de cette espèce. Cette approche occulte l'incertitude associée à la variabilité intra et inter-individuelle de valeurs de densité de bois et ne permet donc pas de propager cette incertitude aux estimations de biomasse. Au cours du chapitre 3, nous définissons un modèle de densité de bois qui permet d'associer à chaque espèce une distribution de densité de bois. Notre modèle ressemble à celui développé au même moment par d'autres auteurs sur une base de données mondiale (Flores & Coomes, 2011; Chave *et al.*, 2009).

Modèle de hauteur

La hauteur est prédite à partir du diamètre de l'arbre. En forêts boréales, il est possible de calibrer des modèles de hauteurs différents pour chaque espèce du

peuplement (Sharma & Parton, 2007). En forêt tropicale, la biodiversité est très importante (plus de 1500 espèces d'arbres en Guyane française). Il est impossible de mesurer assez d'arbres d'une même espèce pour calibrer un modèle de hauteur pour chaque espèce. Les modèles de hauteur en forêt tropicales s'appliquent à tous les arbres d'un peuplement.

Les techniques de mesure des hauteurs d'arbre sont variées : mesure directe avec un grimpeur, laser, triangulation, mesure à l'œil nu... Mais contrairement aux mesures de densité de bois, ces techniques mesurent toutes la même quantité : la hauteur du plus haut élément de l'arbre. Les biais qui peuvent apparaître lors de l'utilisation de l'une ou l'autre des méthodes sont des erreurs de mesures.

Les modèles de hauteurs peuvent être classés en deux catégories : les modèles avec asymptote et les modèles sans asymptote. Dans le matériel supplémentaire du chapitre 3 ainsi que dans le chapitre 4, nous comparons plusieurs formes de modèles. Nos choix nous semblent les plus judicieux pour la forêt guyanaise mais ne sont peut-être pas les meilleurs dans d'autres régions. Le modèle sélectionné au cours de la thèse est un modèle avec asymptote rarement utilisé pour modéliser la hauteur des arbres : le modèle de Michaelis-Menten. Ce modèle est bien adapté pour prendre en compte l'influence de variables environnementales sur les variations de relations entre hauteurs et diamètres (chapitre 4).

Dans le chapitre 3, nous proposons et mettons en œuvre une méthode pour propager les incertitudes issues des prédictions de densités de bois et de hauteurs d'arbres dans les estimations de biomasse. Nous identifions le modèle de biomasse comme source principale d'incertitude.

1.4.2 Les inventaires forestiers

Notre variable d'intérêt, la biomasse s'exprime en masse par unité de surface. Par conséquent, la surface d'une zone inventoriée doit être connue avec précision et l'inventaire exhaustifs à l'intérieur de cette zone. Les inventaires non exhaustifs ne peuvent pas être utilisés comme par exemple certains inventaires à visée botanique (inventaire des espèces présentes) ou d'exploitation forestière (inventaire des espèces commerciales uniquement).

Dans le second chapitre de la thèse, nous explorons les conséquences de plusieurs formes d'inventaires forestiers sur les estimations de biomasse et de biodiversité. Plusieurs techniques d'inventaires classiques sont simulées sur des grandes parcelles inventoriées. Les résultats permettent de choisir des méthodes d'inventaire appropriés aux objectifs. Par contre, nous n'étudions pas les incertitudes associées à la mesure de la surface des parcelles inventoriées.

1.4.3 Extrapolation spatiale

Les différentes stratégies permettant d'estimer la biomasse d'une région sont bien identifiées (Araujo *et al.*, 1999a; Bombelli *et al.*, 2009). Elles peuvent être séparées en deux catégories :

- Les méthodes naïves : les parcelles inventoriées sont représentatives de leur région. La biomasse de la région est donc simplement la biomasse moyenne des inventaires qui y sont réalisés. La fiabilité de cette méthode dépend de l'homogénéité de la forêt de la région. Cette problématique est étudiée dans le chapitre 2.
- Les méthodes basées sur des co-variables : les parcelles inventoriées sont décrites par des variables qui vont servir de prédicteurs en-dehors des zones inventoriées. Cette catégorie contient les méthodes de traitement du signal

de mesures physiques du peuplement (images, radar, Lidar) et les méthodes basées sur des descriptions de l'environnement abiotique des parcelles (sol, pluviométrie, ...).

Il est évident qu'à l'avenir les méthodes de traitement du signal seront les plus efficaces. Le signal réfléchi par la forêt doit permettre de connaître les propriétés de ce peuplement (Goetz *et al.*, 2009). Embarqués dans des satellites, les appareils de mesure nous donneront des mesures de biomasse en temps réel. Bien au point pour les forêts boréales (Muukkonen & Heiskanen, 2007), le dispositif requiert encore des améliorations en forêts tropicales. En effet, les dispositifs classiques basés sur le radar montrent leurs limites sur les fortes biomasses des forêts tropicales (Le Toan *et al.*, 2011). De nouvelles méthodes plus spécifiquement adaptées aux tropiques sont déjà mises en œuvre (Baccini *et al.*, 2012) et donnent des résultats satisfaisants à très grande échelle (chapitre 5). Ce n'est qu'une question de temps avant que de nouvelles méthodes (Sun *et al.*, 2011; Vincent *et al.*, 2012) qui puissent capter des variations de biomasse plus locales soient développées.

Dans le chapitre 5, nous mettons en œuvre la méthode alternative basée sur des covariables environnementales. Cette méthode s'appuie plus sur l'écologie de la forêt et les facteurs environnementaux qui déterminent les caractéristiques du peuplement forestier. La qualité des prédictions de biomasses en dehors des zones inventoriées est donc dépendante de la force de la relation entre la biomasse et les variables environnementales et de notre capacité à comprendre et à modéliser cette relation.

Cependant, les méthodes aéroportées et les modèles sur covariables environnementales ont comme point commun d'utiliser des parcelles de références pour l'apprentissage de leur modèle de biomasse. La mise en place des parcelles d'in-

ventaires et le calcul de leurs biomasses restent requis lors des campagnes de mesure de biomasse aéroportées. Les résultats concernant l'incertitude des prédictions avec notre modèle environnemental pourraient donner des pistes de réflexion pour propager les incertitudes lors de mesures basées sur le traitement de signaux RADAR ou LIDAR.

1.5 Matériel et méthodes

1.5.1 Données

Une attention particulière a été portée aux données utilisées : toutes les données ont été récoltées en Guyane française entre 1972 et 2011. Quand des jeux de données d'origines différentes étaient mélangés, leur cohérence était vérifiée. Cela nous a conduits par exemple à ne pas utiliser certains inventaires forestiers.

Données de biomasse

Nous utilisons les données récoltées pendant le projet ECEREX (Lescure *et al.*, 1983). Sur une parcelle de 1 ha préalablement inventoriée, 361 arbres ont été sélectionnés, abattus, et pesés. Les plus gros arbres n'ont pas été pesés entièrement mais leur masse a été précisément estimée à partir de la forme du tronc et des masses de disques de bois prélevés régulièrement. En plus de la masse, les diamètres et hauteurs de tous les arbres sont connus. La densité de bois n'a pas été mesurée conformément à la définition que nous avons choisi ; elle doit donc être prédite à partir des identifications taxinomiques (260 arbres identifiés jusqu'à l'espèce). Ces données sont représentées sur la figure 1.5.4. Le modèle de biomasse calibré sur ces données est présenté dans le chapitre 3.

Ces données sont les plus importantes car elles contiennent les seules vraies

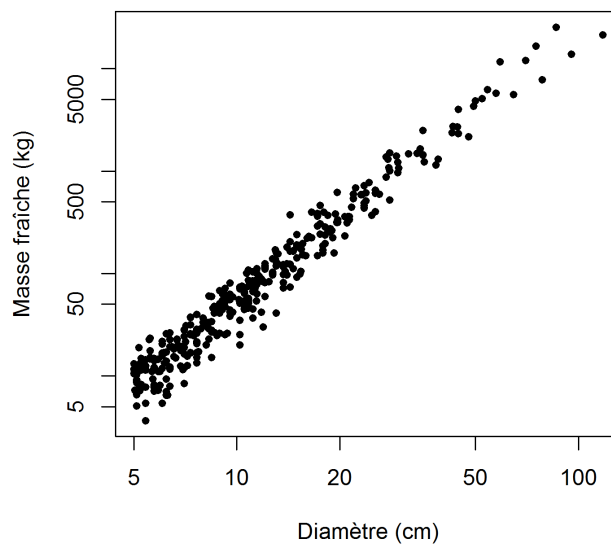


FIGURE 1.5.4 – Données de biomasse : masses des 361 arbres en fonction de leurs diamètres, échelle logarithmique.

valeurs de biomasses des arbres. Toutes les estimations de biomasses découlent des modèles calibrés sur ces arbres pesés. Paradoxalement, ce sont les données les plus anciennes. Ces données sont complexes à récolter (abattage des arbres, pesage) et sont précieuses. Récolter de nouvelles données de masses d'arbres avec un plan d'échantillonnage éclairé par les développements "récents" de la modélisation de la biomasse permettrait des améliorations importantes.

Données de densité de bois

Nous utilisons les données de densité de bois mesurées lors du projet Bridge (Baraloto *et al.*, 2012; Chave *et al.*, 2008). En fait de densité de bois, il s'agit de gravité spécifique (Williamson & Wiemann, 2010). En utilisant une seule base de données, nous évitons les problèmes liés aux multiples définitions et méthodes de mesures de la densité du bois. Les données contiennent 2 504 mesures représentant 466 espèces. Le nombre de mesures par espèce varie de 1 à 50. Un extrait des données est représenté sur la figure 1.5.5. Le modèle de densité de bois calibré sur ces données est présenté dans le chapitre 3.

Données de hauteurs d'arbres

Nous utilisons les données de hauteurs mesurées lors de deux projets différents : le projet Bridge (9 parcelles) (Baraloto *et al.*, 2012) et le projet Amalin (33 parcelles) (Baraloto *et al.*, 2011). Dans chaque parcelle, les diamètres et hauteurs des arbres sont mesurés. Les parcelles sont caractérisées par les variables environnementales décrites ci-après ainsi que par la structure diamétrique du peuplement (proportions d'arbres dans trois classes de diamètres). Ces données sont utilisées pour l'étude des modèles de hauteur dans le chapitre 4. Les données d'une parcelle Bridge sont représentées sur la figure 1.5.6.

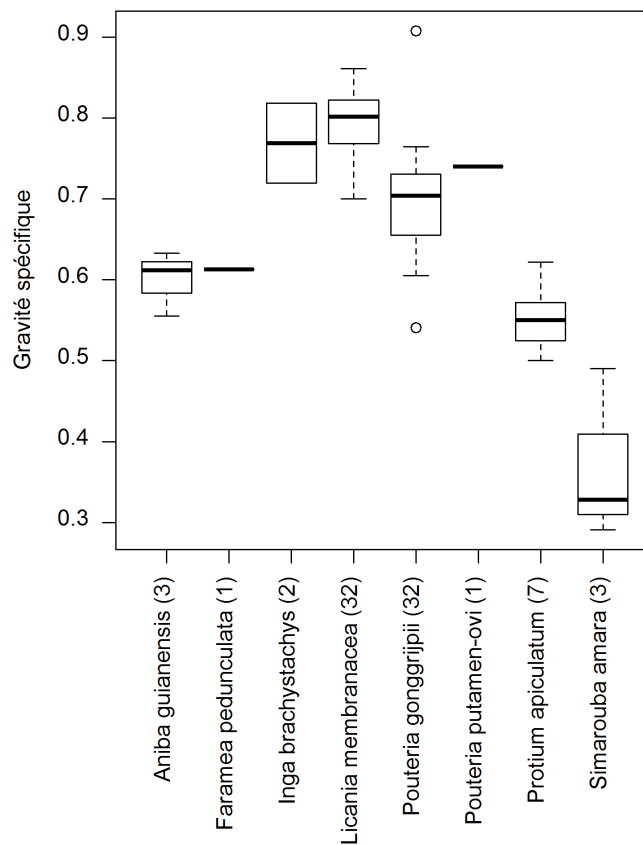


FIGURE 1.5.5 – Données de gravité spécifique : gravités spécifiques de huit espèces. Le nombre entre parenthèses après le nom de l'espèce indique le nombre de mesures réalisées pour cette espèce.

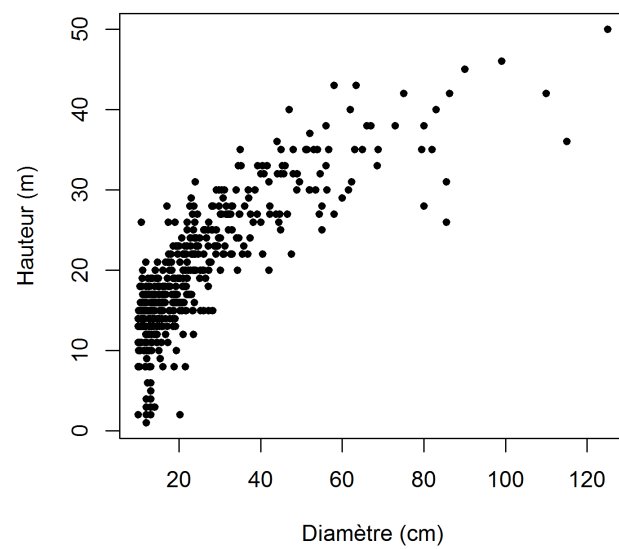


FIGURE 1.5.6 – Données de hauteur : Diamètres et hauteurs mesurées sur la parcelle du projet Bridge située à Lavilette.

Parcelles inventoriées

Pour réaliser la carte de biomasse et étudier les relations entre biomasse et descripteurs environnementaux, nous nous appuyons sur les parcelles forestières issues de 4 projets : l'inventaire papetier réalisés par le CTFT entre 1972 et 1976 (1913 placettes de 0.5 ha) (Guitet *et al.*, 2006), les parcelles témoins du réseau Guyafor (13 parcelles entre 4 et 7 ha) (Blanc *et al.*, 2009), les parcelles du projet Bridge (9 parcelles de 1 ha) (Baraloto *et al.*, 2012), et les parcelles du projet Amalin (33 parcelles de 0.5 ha) (Baraloto *et al.*, 2011). Ces parcelles sont situées dans la partie nord de la Guyane française. Une carte indique leurs positions dans le chapitre 5. Les parcelles du projet Amalin ont été réalisées selon le protocole décrit au chapitre 2.

Une analyse en composantes principales sur les variables décrivant les parcelles (environnement et structure diamétrique) permet de s'assurer que les inventaires sont bien cohérents entre eux (figures 1.5.7 et 1.5.8). Certains inventaires du projet Amalin se détachent nettement (figure 1.5.7, en bas à droite). Il s'agit d'inventaires réalisés sur des inselbergs (plutons granitiques qui émergent de la forêt). Ces parcelles sont bien identifiées comme exceptionnelles par les variables environnementales.

Selon l'inventaire réalisé (avec ou sans hauteurs, avec ou sans botanique), le processus d'estimation de la biomasse n'est pas toujours le même. Le processus utilisé pour chaque inventaire est explicité dans le chapitre 5.

Variables environnementales

Géologie : Nous utilisons la carte de substrat géologique produit par le BRGM (Delor *et al.*, 2001). La carte a été simplifiée pour ne garder que cinq grandes classes de roches : les sédiments récents, les sédiments volcaniques, les

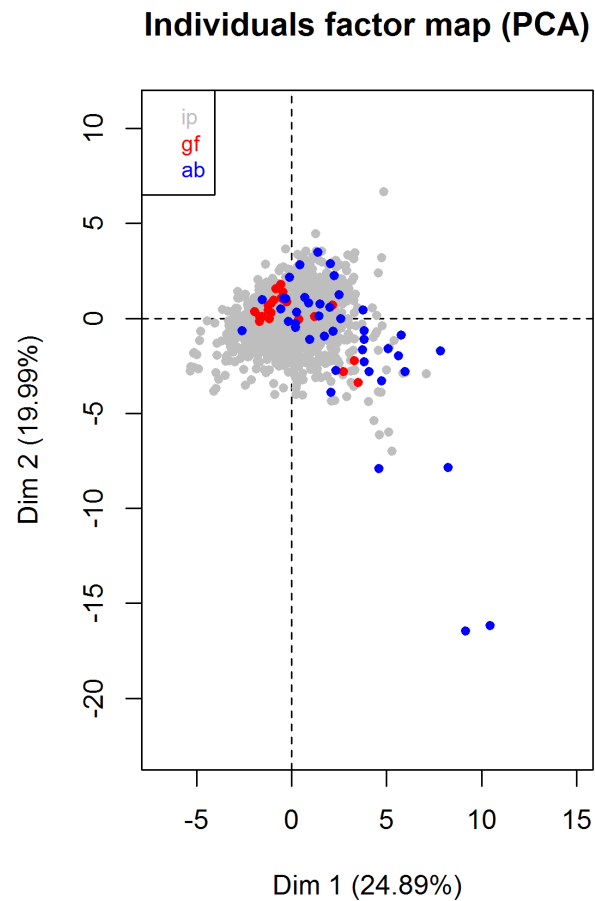


FIGURE 1.5.7 – Analyse en composantes principales des parcelles inventoriées - graphique des individus. En gris, les parcelles de l’inventaire papetier ; en rouge les parcelles de Guyafor ; en bleu les parcelles des projets Bridge et Amalin.

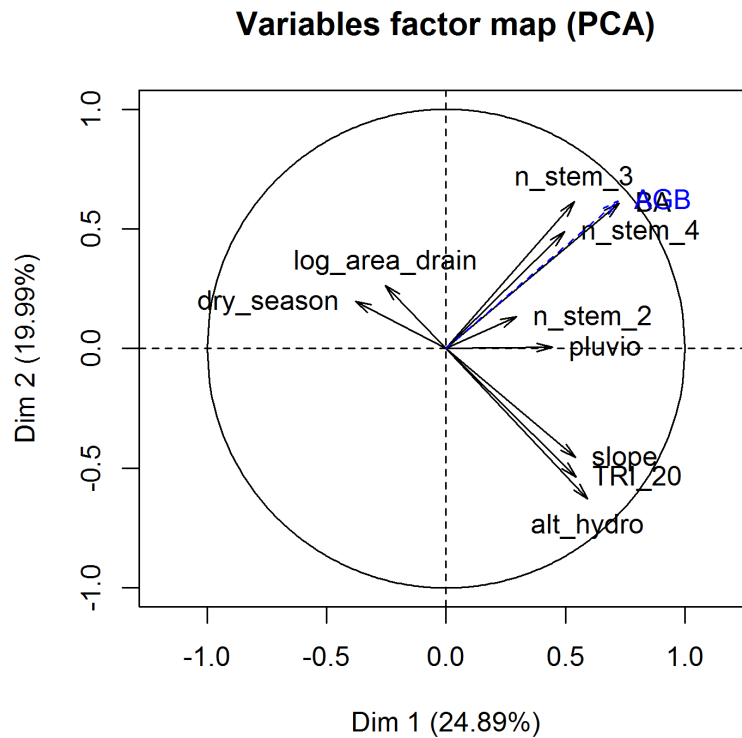


FIGURE 1.5.8 – Analyse en composantes principales des parcelles inventoriées - graphique des variables. La biomasse, en bleu, est une variable supplémentaire. "n_stem_2", "n_stem_3", et "n_stem_4" sont les proportions d'arbres dans les classes de diamètres $[20, 40[$, $[40, 60[$, et plus de 60 cm. "BA" est la surface terrière. "dry_season" et "pluvio" représentent respectivement l'indice de saisonnalité et la pluviométrie moyenne annuelle. "TRI_20", "slope", "log_area_drained" et "alt_hydro" représentent respectivement le Terrain Ruggedness Index, la pente, le log de l'aire drainée, et l'altitude par rapport au cours d'eau le plus proche.

granites, les gabbros, et les gneiss. Cette simplification est nécessaire pour que chaque classe de géologie soit échantillonnée de manière satisfaisante. La carte est visible dans le chapitre 5.

Climat : Les variables climatiques sont calculées à partir des précipitations journalières des 10 dernières années selon le satellite de la mission TRMM de la NASA. La carte des précipitations annuelles moyennes est dans le chapitre 5. L'indice de saisonnalité est le nombre moyen de mois pendant lesquels les précipitations sont inférieures à 100 mm.

Topography et hydrologie : Un modèle numérique de terrain à 90m est utilisé pour calculer différents indices décrivant le relief (pente, Terrain Ruggedness Index) et le fonctionnement hydrique (altitude par rapport au cours d'eau le plus proche, aire drainée).

En plus de ces variables environnementales, nous utilisons une carte des faciès forestiers de la Guyane française (Gond *et al.*, 2011). Cette carte a été générée à partir d'images satellites et ne s'intègre donc pas vraiment à nos autres données. Nous avons toutefois choisi de l'inclure dans la mesure où elle pourrait permettre d'améliorer sensiblement la qualité des estimations de biomasse, ce qui est un objectif important de notre travail.

1.5.2 Méthodes statistiques

La majorité des modèles utilisés au cours de la thèse ont été calibrés par des méthodes bayésiennes. Ces méthodes permettent l'inférence de modèles intégrant de l'information *a priori* dans une structure hiérarchique (modèle de densité de bois, chapitre 3). Les méthodes bayésiennes permettent aussi l'inférence de modèles complexes (modèles de hauteur, chapitre 4) sans qu'il soit nécessaire de maximiser la fonction de vraisemblance.

De plus, les méthodes bayésiennes sont très bien adaptées à notre objectif de propagation des incertitudes. Dans le paradigme bayésien, la distribution de probabilité d'un paramètre représente la confiance que l'on a dans la valeur de ce paramètre. Nous propageons l'incertitude des paramètres des modèles et des variables prédites par ces modèles selon un processus de Monte-Carlo, en tirant des valeurs dans leurs lois de probabilité.

Seul le modèle spatial de biomasse (chapitre 5) a été calibré avec des méthodes fréquentistes. Les données trop volumineuses ne permettaient pas d'échantillonner *a posteriori* les distributions des biomasses sur la carte de la Guyane. Pour ce modèle, nous avons utilisé le package *geoR* (Ribeiro Jr. & Diggle, 2001). Programmer l'inférence nous-mêmes nous aurait peut-être permis de l'adapter plus précisément à notre problématique et d'optimiser ainsi les calculs.

Chapitre 2

Estimations de biomasse et de biodiversité en forêt tropicale : comparaison de différentes méthodes d'inventaires

Plusieurs méthodes existent pour mettre en place une parcelle forestière. Dans le cadre de la mise en place d'un nouveau type de parcelle (Gentry amélioré), nous avons comparé les performances de cinq méthodes d'inventaires différentes. Ces méthodes sont des inventaires exhaustifs sur des surfaces précises et sont donc adaptés à l'estimation de la biomasse : rectangles de 0.1 ha, carrés e 0.5 ha, carrés de 1ha, Gentry original (0.1ha éclaté) et Gentry modifié (0.5ha éclaté). L'objectif est de savoir si certaines parcelles, par leurs formes et leurs surfaces, sont plus représentatives que d'autres de la forêt dans laquelle elles sont placées en termes de biomasse et de biodiversité.

Pour comparer les différentes méthodes d'inventaires, nous les avons simulées

dans des grandes zones inventoriées. Ces grandes zones ont été choisies pour représenter différents faciès forestiers d'Amérique du sud (station des Nouragues et de Paracou en Guyane, Barro Colorado Island au Panama, Yasuni en Equateur, et Luquillo à Puerto Rico). Pour répondre à la problématique, chaque grande zone est considérée comme une région dont on cherche à estimer la biomasse et la biodiversité. Pour chaque méthode d'inventaire, nous observons l'évolution de la précision des estimations de biomasse et de biodiversité quand le nombre de parcelles simulées augmente.

A surface égale, la forme de la parcelle a finalement peu d'influence sur l'estimation de la biomasse et de la biodiversité. Cependant, des grandes différences existent quant à l'effort requis pour réaliser les inventaires des différentes parcelles. Dans ce contexte, la nouvelle forme proposée apparaît avantageuse pour estimer de façon rapide à la fois la biomasse et la biodiversité. Par contre, les parcelles Gentry, par la multiplication des petits transects, semblent inappropriées pour des inventaires réguliers dans le temps.

Dans ce chapitre, la biomasse est estimée à partir d'un modèle pan-tropical (Chave *et al.*, 2005). Il ne s'agit pas encore de réaliser des estimations de biomasses précises et associées à leur incertitude mais d'étudier l'impact de la structuration spatiale des données biologiques sur la précision des estimateurs.

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RAPID SIMULTANEOUS ESTIMATION OF ABOVEGROUND BIOMASS AND TREE DIVERSITY ACROSS NEOTROPICAL FORESTS: A COMPARISON OF FIELD INVENTORY METHODS

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LRH: Baraloto *et al.*

RRH: Plot Methods in Tropical Forests

ABSTRACT

A standardized rapid inventory method providing information on both tree species diversity and aboveground carbon stocks in tropical forests will be an important tool for evaluating efforts to conserve biodiversity and to estimate the carbon emissions that result from deforestation and degradation (REDD). Here we contrast five common plot methods differing in shape, size and effort requirements to estimate tree diversity and aboveground tree biomass (AGB). We simulated the methods across six Neotropical forest sites that represent a broad gradient in forest structure, tree species richness and floristic composition, and we assessed the relative performance of methods by evaluating the bias and precision of their estimates of AGB and tree diversity. For a given sample of forest area, a 'several small' (< 1 ha) sampling strategy led to a smaller coefficient of variation in the estimate of AGB than a 'few large' one. The effort (person days) required to achieve an accurate AGB estimate (<10% coefficient of variation [CV]), however, was greater for the smallest plots (0.1 ha) than for a compromise approach using 0.5 ha modified Gentry plots, which proved to be the most efficient method to estimate AGB across all forest types. Gentry plots were also the most efficient at providing accurate estimates of tree diversity (<10% CV of Hill number). We recommend the use of the 0.5 ha modified Gentry plot method in future rapid inventories, and we discuss a set of criteria that should inform any choice of inventory method.

Key words: Barro Colorado Island; biodiversity assessment; carbon stocks; Luquillo; Nouragues; Paracou; permanent plot; REDD; tropical rain forest; Yasuní.

INTRODUCTION

Tropical forests have long been recognized to harbor a significant proportion of global biodiversity (Myers *et al.* 2000; Gaston 2000), with at least a third of all higher plant species occurring in the Neotropics and 12 percent in Amazonian forests alone (Gentry 1982). Recently, the conservation value of tropical forests has been expanded to include their important contribution to carbon storage and potential mitigation of global climate change (Gullison *et al.* 2007). Tropical forests are estimated to account for an estimated 229 Pg of aboveground biomass carbon (Baccini *et al.* 2012), or nearly half of that estimated to be stored in vegetation worldwide (Houghton 2005), with remote sensing and ground based estimates of carbon in the Amazon basin alone varying from 86–96 Pg (with about 20% uncertainty) (Malhi *et al.* 2006; Saatchi *et al.* 2007).

Rising rates of deforestation and degradation in tropical forests have underlined the need for information on the spatial distribution of ecosystem properties, including biodiversity and carbon stocks, to assist managers when setting aside zones for protection (Venter *et al.* 2009, Saatchi *et al.* 2011). Despite substantial efforts by researchers over the past 30 years, the structure and composition of large areas of tropical forests remains poorly (or un-) studied (Foster *et al.* 1998, Feeley & Silman 2011), thereby complicating management decisions in many tropical countries. Much of the effort necessary to inventory sites of the highest priority is expended on travel, such that time in the field becomes extremely valuable. A standardized rapid inventory method that provides information on *both* biodiversity and carbon stocks will thus represent an important tool to enhance our ability to maximize biodiversity conservation and to help quantify potential carbon emissions that result from deforestation and degradation (REDD). A standardized rapid inventory method will also be critical in the immediate future to provide calibration points for remote sensing methods estimating forest carbon stocks (Asner *et al.* 2010, Saatchi *et al.* 2011) and floristic composition (Asner & Martin 2011). Here we test a variety of plot methods to establish the most accurate and efficient way to reach this goal.

The most widespread forest inventory method used for both tree diversity and AGB estimates is the 1 ha plot (*e.g.*, Stropp *et al.* 2009, Phillips *et al.* 2009), as initially recommended by the Food and Agriculture Organization (FAO 1981). Recent studies, however, have challenged whether these plots are the most appropriate size and shape to measure floristic composition because they may miss rare species or over-represent spatially aggregated species (Phillips *et al.* 2003). Critiques have also been leveled against the AGB estimates from 1 ha plots because the plots may be too small to accurately characterize carbon stocks for static measures (Wagner *et al.* 2010), or to monitor their temporal dynamics (Chambers *et al.* 2009). Several alternatives to 1 ha plots have been suggested, differing primarily in their sizes, shapes, and the minimum size of trees inventoried (Table 1). Among these is the Gentry plot method (Boyle 1996, Phillips *et al.* 2003), a modified version of which has been used to estimate AGB across contrasting Amazonian forests (Baraloto *et al.* 2011).

TABLE 1. *Inventory methods commonly used for surveying of aboveground biomass and/or plant diversity in Neotropical forests.*

Method	Area covered	Area inventoried		dbh min (cm)	Permanent	Effort (person-days)†	Existing plots in Neotropics		Reference
Gentry Plot*	2 ha	0.1 ha	2.5	No	7	> 800		Boyle 1996, Phillips 2003	
Whittaker Plot*	0.1 ha	0.1 ha	2.5	No	7	At least 100		Campbell et al. 2002	
Modified Gentry Plot*	2 ha	0.5 ha	Variable	Yes	8	160		Baraloto et al. 2011	
0.5 ha Plot*	0.5 ha	0.5 ha	2.5	Yes	15	unknown			
1 ha Plot*	1 ha	1 ha	10	Yes	25	> 750		FAO 1981	
Circular plot	0.28 ha	0.28 ha	10	Yes	5	> 130		Asner et al. 2010	
Brazil Forest Service	4 ha	0.4 ha	Variable	Yes	5-10	thousands to be implemented		D. Piotto, pers. comm.	
NFI plot									
large CTFS Plot	Up to 52 ha	Up to 50 ha	1	Yes	>500	9		Condit 1995	
Ad hoc botany	Variable	NA	NA	No	Variable	NA		Hopkins 2007	

* Indicates method analyzed in this study

† see text for details of calculations

Sampling methods can be evaluated based on two concepts that together define the accuracy of their estimators: *sampling bias*, which refers to deviations of estimates from the true value; and *sampling precision*, which refers to the breadth of variation in the estimate (Walther & Moore 2005).

(1) Sampling bias for estimates of AGB may occur, for example, because allometries for tree biomass were not calibrated in the site where they are applied (Clark 2000). The choice of plot method should not introduce bias into estimates of AGB as each plot represents a sample from the biomass distribution of the considered area. The mean of the samples is an unbiased estimator of the mean AGB value of the area. It supposes that the plots are placed randomly with equal probability. In contrast, sampling bias represents an important issue in estimating species richness, because methods contrast markedly in the proportion of species present in a site that are sampled (Brose *et al.* 2003, Walther & Moore 2005, Beck & Swangforth 2010).

(2) Sampling precision represents the reduction of variance of AGB and species occurrences between plots. This variability is influenced both by spatial variation of AGB and species distributions; as well as by plot characteristics (size, shape; Laurance *et al.* 1999).

The most efficient protocol for assessing tree species diversity and AGB simultaneously will reach a compromise between the accuracy of both estimators (in terms of bias and precision) versus the amount of resources (time and/or money) necessary to implement the protocol (Phillips *et al.* 2003, Abrahamson *et al.* 2011). Efficient plot-based sampling is especially important for rapid inventories to assess protected areas (Foster *et al.* 1998; Higgins & Rukolainen 2004) and for the calibration of remote sensing analyses across large areas (Asner *et al.* 2010, Saatchi *et al.* 2011). Yet to date no empirical comparison is available from which to draw inferences for choosing an appropriate protocol across the many different forest types that exist in the tropics.

Here we use a simulation approach to estimate AGB and tree biodiversity within large permanent plots from six Neotropical forests representing a broad gradient in tree species richness (88–821 species among trees ≥ 10 cm in diameter at 1.3 m height [dbh] per 50 ha plot) and forest structure (AGB of 283–494 Mg ha⁻¹) (Table 2). In particular, we address three objectives. First, we test a range of plot sizes and shapes to determine the most accurate (least bias and greatest precision) and most efficient (accuracy per unit effort) method to estimate AGB and tree biodiversity. Second, we evaluate whether there exists a general trade-off among methods in the accuracy of information they provide for tree diversity versus aboveground biomass estimates. Third, we analyze the extent to which different inventory methods may be appropriate among forests differing in structure and floristic composition.

TABLE 2. Description of the permanent plot sites used in this study. Precise floristic composition and data for stems <10 cm dbh were only available for the first three sites.

Site	Area (ha)	Dimensions (m*m)	Year of census	AGB (Mg ha-1)	Species richness (≥ 2.5 cm dbh)	Species richness (≥10 cm dbh)	Community wsg*	Stem Density (≥2.5 cm dbh) (ha-1)
BCI (Panama)	50	1000*500	2005	322	276	228	0.545	2388
Luquillo (Puerto Rico)	16	500*320	2000	360	139	88	0.604	2084
Yasuni (Ecuador)	25	500*500	2003	283	1038	821	0.588	3233
Nouragues – GP (French Guiana)	10	1000*100	2008	443	-	†	0.782	-
Nouragues – PP (French Guiana)	12	300*400	2008	494	-	†	0.782	-
Paracou (French Guiana; 6 plots)	37.5	250*250	2009	432	-	†	0.782	-

*wsg values from CTFs plots were applied as site-level means from Stegen et al. (2009)

† taxonomic inventories of the complete study area are not yet completed

METHODS

Estimating biodiversity and carbon stocks

Our dataset comprised Neotropical forest sites including (1) permanent plots of at least 10 ha to permit within-plot sampling of all methods and (2) reliable data for tree spatial locations and dbh for carbon estimates and species identifications for biodiversity estimates. For each site we chose the most reliable recent inventory census for that plot (Table 2).

At each site, we considered five possible plot methods among those most commonly used in tropical forests (Table 1). Three of these methods employ contiguous rectangles of different shapes, and two (Gentry plots) are composites of belt transects across a 2 ha area. These Gentry plots group either ten 2 m × 50 m belt transects (modified Gentry plot; Phillips *et al.* 2003) or an extension of these for AGB estimates to 10 m × 50 m transects for larger trees ≥ 20cm dbh (revised 0.5 ha modified Gentry plot; Baraloto *et al.* 2011, inspired by Phillips *et al.* 2001). Comparing the composite Gentry plots with rectangular subplots of 0.5 or (respectively 0.1) hectare of the same area thus allows us to evaluate the influence of plot shape (contiguous versus spread) on the accuracy of the forest descriptors. Although the methods considered here are by no means exhaustive, they represent the large majority of published regional studies on AGB and tree diversity in the Neotropics (Table 1). We did not consider circular plots that have been employed in temperate forests such as the USDA Forest Service’s Forest Inventory and Analysis program (Lichstein *et al.* 2010). Circular plots are widely regarded as difficult to demarcate in the dense understory of tropical forests (Adler & Synott 1992), although a few research groups continue to use them for calibration of remote sensing estimates of AGB (e.g., Asner *et al.* 2010).

We evaluated the individual tree AGB using the formula of Chave *et al.* (2005) for moist tropical forests without tree height data, as the heights were not available for all plots.

$$AGB_i = wsg_i \times e^{(-1.499 + 2.148 \times \log(DBH_i) + 0.207 \times (\log DBH_i)^2 - 0.028 \times (\log DBH_i)^3)}$$

with DBH_i of tree i in cm and wood specific gravity (wsg_i) of tree i without dimension. Our simulations were conducted following Stegen *et al.* (2009) as site-level means, with values for Paracou and Nouragues calculated by referencing a local wood density database with species composition (Sarmiento *et al.* 2011). We note that the Chave *et al.* (2005) allometry without height may overestimate AGB in forests where tree height is lower for a given tree dbh than the forests from which datasets were collected (Feldpausch *et al.* 2011), but this should not affect the results we present here, even though it may exaggerate spatial variability in stands with skewed dbh structures.

For biodiversity, we compared 1 ha plots and the 0.1 ha plots of different shapes (single rectangle vs. Gentry multiple transect) as these are the two most popular methods currently used to estimate biodiversity (Campbell *et al.* 2002, Phillips *et al.* 2003, Stropp *et al.* 2009). The 0.5 ha modified Gentry plot was designed to extend sampled surface area only for AGB estimates and thus uses floristic information only from its 0.1 ha Gentry plot core. We evaluated estimates of biodiversity including total species number S in each sample (Walther & Moore 2005) as well as Hill numbers which represent the number of equally-abundant species yielding the same diversity as the sample (Jost 2006).

Simulating different plot methods

We simulated the five plot methods in each large permanent plot. For each plot method, we partitioned the large permanent plot into simulated subplots of different sizes and shapes, to cover the largest possible area of the permanent plot with no subplot overlap. We sampled from the resulting subplot units with replacement to obtain a statistical population for each plot method. Depending on the size of the permanent plot (Table 2) and the plot method simulated (Table 1), we were able to place at least ten simulated plots in each permanent plot. For each plot method in each permanent plot, we generated randomly 1000 populations for a series of 1–20 plots (depending on plot method). We calculated estimates of AGB and biodiversity (S and Hill number) for each population.

Statistical methods

We evaluated the relative performance of the five methods using measures of bias and precision. Our analysis is not completely symmetrical because measures of bias are not relevant for comparing plot methods in their estimates of AGB. The true value of AGB in a regional site is the mean of a distribution of sampling points in that region; and randomly-placed plots, no matter the method used, will provide unbiased estimates of this mean, even if they may be imprecise. In contrast, the true value of diversity for a regional site is a parameter for which sampling methods may be biased (Walther & Moore 2005). We measured bias in estimates of diversity using a transformed value of scaled mean error referred to as the percent of actual richness (PAR; Baltanas 1992) estimated from the entire larger permanent plot.

We also measured precision for both AGB and diversity using the coefficient of variation (CV) as a normalized measure of dispersion. We considered an accurate estimate for biomass and Hill numbers to be achieved when the CV was less than 10% of the mean (Wagner *et al.* 2010).

We compared among plot methods in several ways. Estimates of AGB are reported relative to surface area rather than number of plots, and so we retained this presentation to permit subsequent interpretations based on the shape and number of simulated plots. For example, an area of 2 hectares can be achieved with two simulated plots of 1 hectare, or four simulated plots of 0.5 hectares, or 20

simulated plots of 0.1 hectares. For biodiversity, we also made calculations based on the total number of individuals sampled (Magurran *et al.* 2010, Gotelli & Colwell 2010).

To compare the efficiency among different methods, we built CV models using one predictor, the *Effort*. *Effort* is defined as the number of person-days required to implement each plot, estimated based on the lead author's experience with different research teams in five countries across the Amazon (Table 1). We considered an average level of competence for a field research team relative to spatial orientation for mapping and measuring trees and botanical knowledge for tree sampling and identification, following criteria implemented by Phillips *et al.* (2003), including tree dbh measures and mapping, assignment to morphospecies, field preparation of herbarium vouchers, and organization of field notebooks. Those authors report an average of 4.6 person-days for a 0.1-ha Gentry plot and 28.3 days for a 1-ha plot in Peruvian forests, which are faster times than we have observed across the region (7 and 35 person-days, respectively), and with a more skewed ratio (Gentry plots are completed more than 6 times faster than 1-ha plots in their study vs. 5 times faster in ours; Table 1).

We defined the CV Effort model following Wagner *et al.* (2010):

$$CV = \alpha \times Effort^{\beta} \times \varepsilon$$

ε being the error term of the model. It can be transformed to

$$\log(CV) = \log(\alpha) + \beta \times \log(Effort) + \log(\varepsilon)$$

with $\varepsilon \sim N(0; \sigma^2)$ to achieve linearity. When predicting *Effort* required to reach a target CV, note that because the exponential of the error distribution centred on 0 is not exactly centred on 1, the back-transformation of the log scale was appropriately corrected.

RESULTS

Aboveground biomass (AGB) estimates

The relative performance of methods for estimating AGB was largely consistent among the six forests. In general, multiple smaller plots (< 1 ha) performed much better than fewer larger plots (1 ha); that is, for a given surface area sampled, the use of multiple smaller plots resulted in a smaller coefficient of variation in the estimate of AGB (Fig. 1). The 0.5 ha modified Gentry plots provided an exception to this rule, outperforming or equalling the performance of 0.1 ha plot methods in five of the six sites (all but BCI). For the plots sampling 0.1 ha, the rectangular format (part of the Whittaker plot, Campbell *et al.* 2002) outperformed the original Gentry plot (0.1 ha) in three sites (BCI, Luquillo,

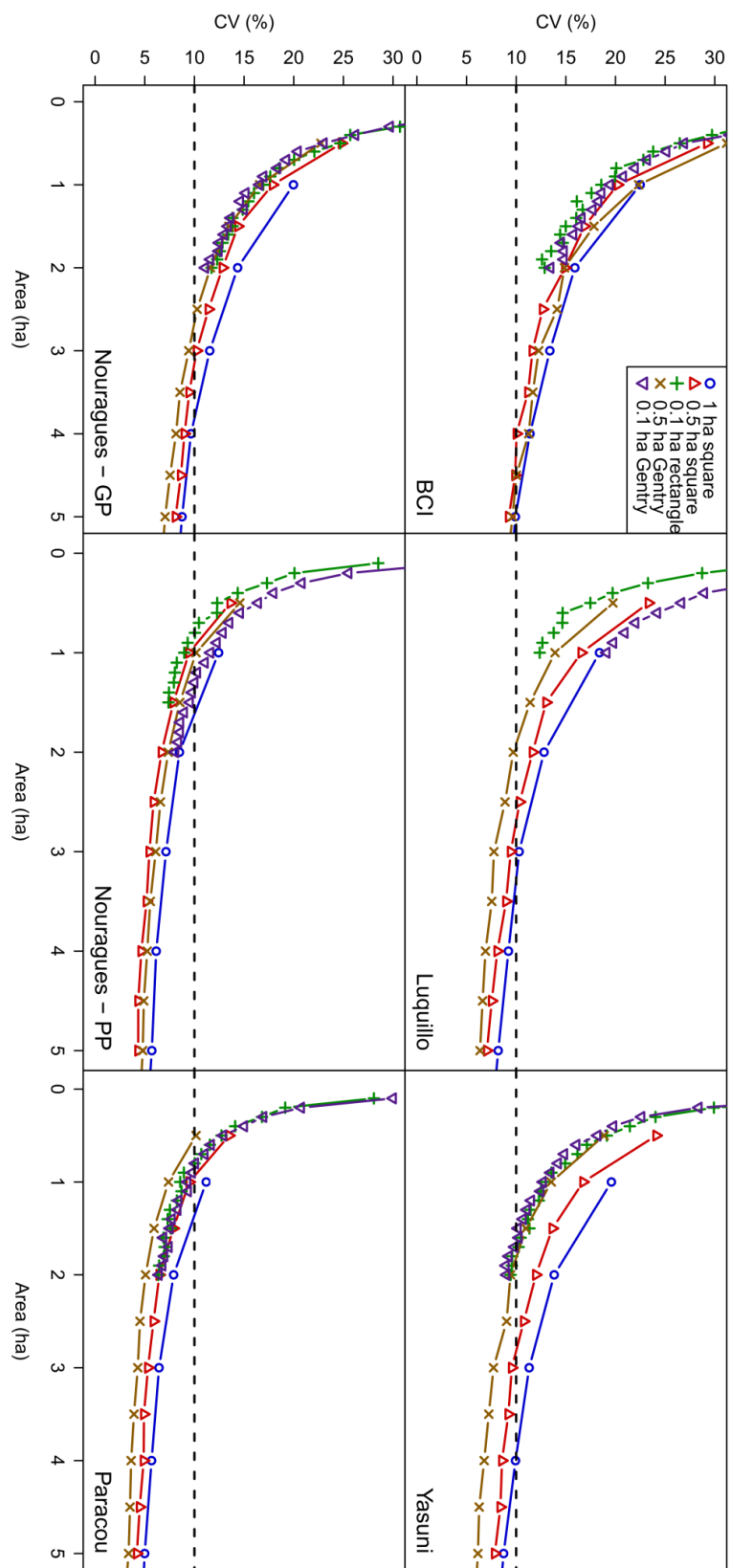


FIGURE 1. The relative precision of five plot methods (see Table 1 for full descriptions) for estimating AGB across six Neotropical forests. Each point represents 1000 simulations of each plot method in each forest site. Reference lines indicate an accepted minimum accurate performance at a CV of 10 percent.

Nouragues PP). In contrast, the 0.5 ha Gentry plot outperformed the square 0.5 ha plot in all sites except BCI.

When translated into the actual effort required to achieve an accurate estimate of site AGB ($< 10\%$ CV), the disadvantage of installing multiple smaller plots becomes apparent, with consistently greater effort required to realize accurate AGB estimates using 0.1 ha plots of any shape (Fig. 2). The 1 ha plots, despite their relatively high cost to implement (Table 1), were more efficient to inventory than the smallest plots, although 1 ha plots were still inferior to the 0.5 ha modified Gentry plots. The 0.5 ha modified Gentry plots consistently emerge as the best compromise when compared to all other methods, with the lowest overall effort necessary to accurately estimate AGB.

Although the relative performance of methods for AGB was consistent among sites, the effort necessary to achieve accurate measurements of AGB ($< 10\%$ of CV) varied widely across different Neotropical forests. At Paracou, for example, an accurate estimate of AGB can be obtained with a single 0.5 ha modified Gentry plot (8 person days), whereas at BCI a minimum of 32 person-days, and four 0.5 ha Gentry plots, would be necessary (Fig. 2).

Tree diversity estimates

Reliable floristic data was available from three of the six sites (BCI, Luquillo and Yasuní), for which species-individual accumulation curves for different plot methods are presented in Figure 3. The smaller plots clearly sample a larger proportion of the overall flora in each of the three sites than do the 1 ha plots. At BCI, however, the composition of trees $\geq 10\text{cm}$ dbh has more balanced relative abundances, such that the Hill number is actually larger than that of the community of trees $\geq 2.5\text{ cm}$ dbh (Fig. 3). As a consequence, 1-ha plots may actually overestimate the total diversity of this site, and smaller plots may underestimate diversity by sampling dominant species, depending on the target community of interest. Between the two 0.1 ha smaller plot methods differing in shape (rectangle vs. Gentry), little difference in sampling performance was apparent in any of the three sites (Fig. 3).

The three plot methods differed substantially in the precision of estimates for tree diversity. Across the three forests, the Gentry plots were the most precise, and the 1 ha plots were the least precise (Fig. 4). To assess the relative performance of plot methods at estimating tree diversity, we considered a precision of 10 percent CV to be acceptable. The smaller plot methods outperformed the 1 ha plots in the effort required to obtain estimates of tree diversity with this precision (Fig. 5). Across all three forests, the Gentry plots outperformed the 0.1 ha rectangular plots in estimating the Hill number, indicating an advantage of sampling a larger overall area despite the accompanying moderate additional cost of increased time investment.

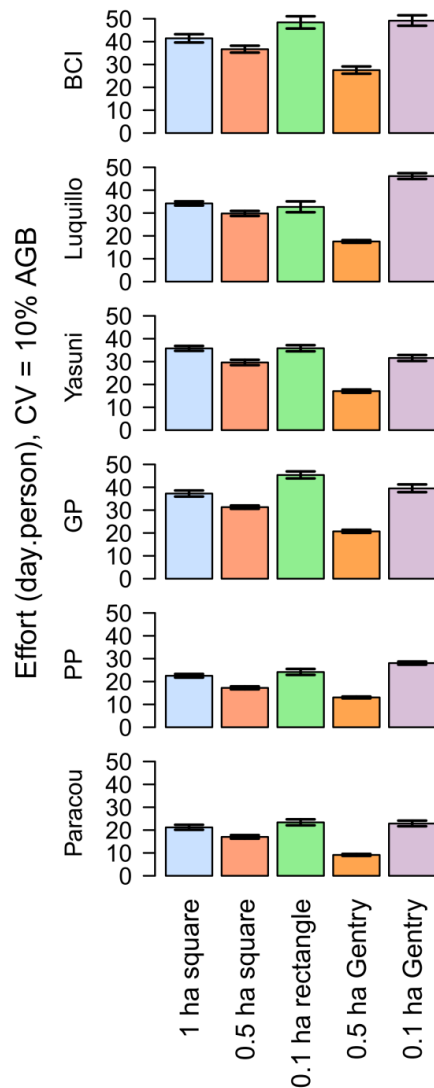


FIGURE 2. The sampling effort (in person-days) required to achieve accurate estimates of AGB (maximum of 10% CV) across six Neotropical forests using five different plot methods. Shown are the mean values (with 5 and 95 % confidence intervals) of 1000 simulations of each plot method in each forest site.

DISCUSSION

We found that one method, the modified 0.5 ha Gentry plot, outperformed all other methods for both accurate AGB and plant diversity estimates. The modified 0.5 ha Gentry plots were the most efficient method for estimating AGB across six forest types varying in structure and floristic composition (Fig. 3). Moreover, the 0.1 ha Gentry plot that forms the core of this approach is also the most efficient method for estimating tree biodiversity across three forests differing widely in species diversity (Fig. 5). We recommend this method receive serious consideration for future rapid inventories in tropical forests. Our recommendation should be weighed in light of the limitations of our study, in addition to other factors involved in research and monitoring studies in tropical forests that we discuss below.

AGB and tree diversity admittedly do not describe all of the ecosystem properties that managers might need when deciding which tropical forest areas to protect. First, biodiversity clearly encompasses more than tree species diversity. Groups such as birds, butterflies, and beetles have been suggested to be more appropriate than trees as overall indices of site biodiversity to determine conservation priorities (Schulze *et al.* 2004, Gardner *et al.* 2008). Nevertheless, vegetation plots provide an important foundation for complementary inventories of other groups, and larger contiguous plots provide the important benefits of extensive mapped areas with associated forest structure and floristic data (Condit 1995). Smaller plot methods can also provide the basis for inventories of other taxonomic groups, with appropriate protocols in place for both contiguous and aggregate plots. For example, in French Guiana we place the 200 m base trail of our 0.5 ha modified Gentry plots along the 4 km trails used for mammal, bird and insect surveys (de Thoisy *et al.* 2008) to permit overall site diversity to be estimated rapidly and accurately.

A biodiversity index such as plot-level richness, Shannon's entropy or the associated Hill number may also not be the most suitable botanical information for forest managers to prioritize sites for protection (Hopkins 2007). This is primarily because the presence of rare species with limited distribution may be more effectively recorded through *ad hoc* sampling rather than with fixed inventory plots (Foster *et al.* 1998; Gordon & Newton 2006; Hopkins 2007), though with *ad hoc* sampling no related estimates of forest structure or quantitative comparisons among sites would be possible. A potential compromise our team has implemented with 0.5 ha modified Gentry plots in French Guiana and Peru is to add *ad hoc* sampling for the entire forest, so that a larger species occurrence list with herbarium vouchers can be produced in addition to the quantitative plot data. The intensive sampling of very large plots appears to capture rare species well (Valencia *et al.* 2004) with an added benefit that permanently marked individuals can be collected at some point with flowers or fruits.

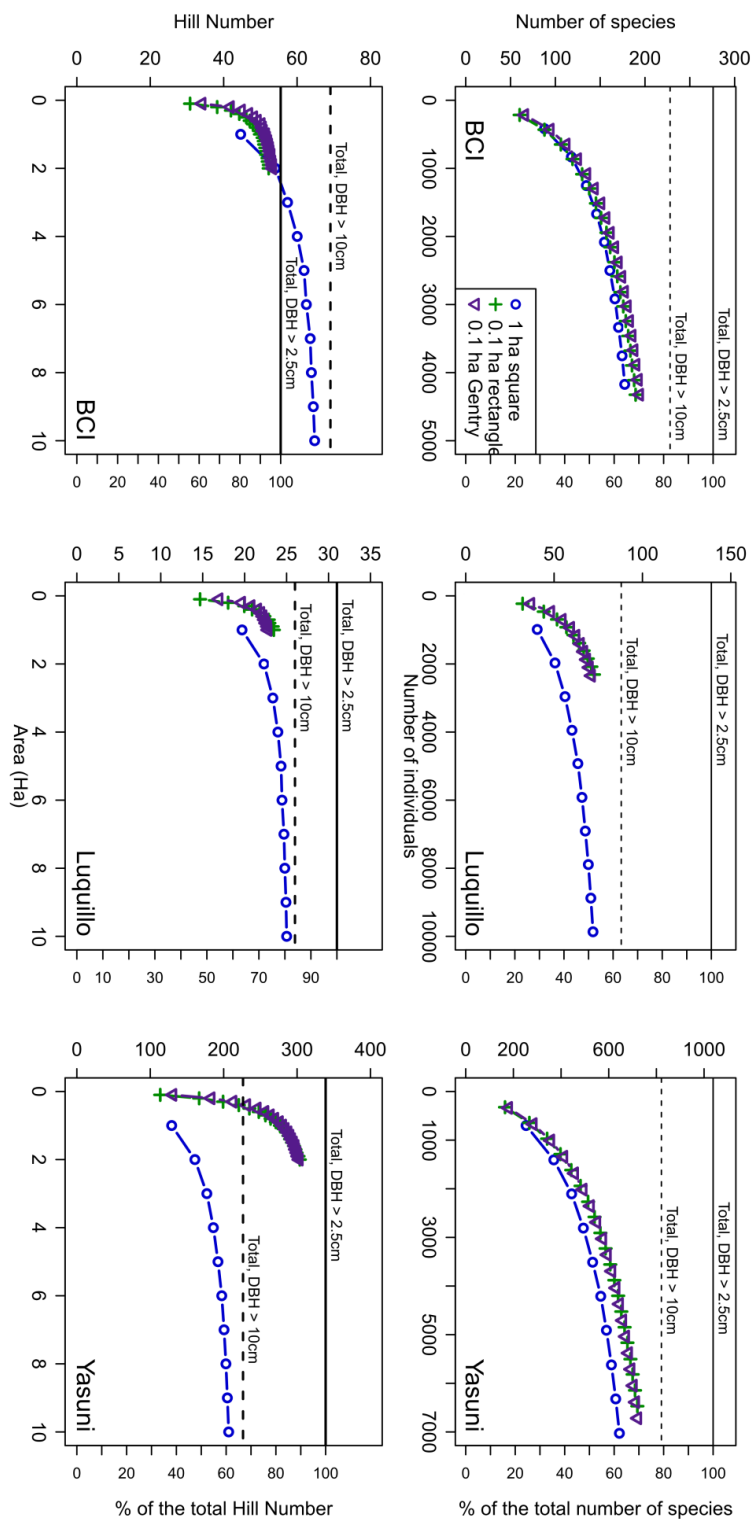


FIGURE 3. Tree diversity estimates from simulated samples of three plot methods across three Neotropical forests. Each point represents 1000 simulations of one of three plot methods in each forest site. Reference lines indicate the total number of species or the Hill number equivalent recorded in each forest at the two minimum size criteria for different plot methods (see Table 1). The percent of actual richness (PAR) is indicated on the second y-axis for reference. Note that the 1-ha plot method estimates tree diversity for stems ≥ 10 cm dbh, whereas the other two methods estimate diversity of stems ≥ 2.5 cm dbh.

Smaller plots with lower than 10 cm minimum tree diameter requirement have the advantage of providing information on a suite of species that are not likely to grow into the larger size classes often used in standard 1 ha plots (see Fig. 3). Smaller plots, however, often do not provide as complete a sample of tree species as do 1 ha plots (Phillips *et al.* 2003) or larger plots that are crucial for long-term monitoring of species spatial and temporal dynamics and species interactions (Condit 1995). Our analysis of the BCI dataset demonstrates how this choice of minimum diameter can influence interpretations. BCI has a relative ratio of overall richness between communities with minimum diameters of 10 cm vs. 2.5 cm that is only slightly higher than that of Yasuní (83 vs. 79%; Table 1). The larger tree community, however, comprises fewer dominant species there, such that 1 ha plots would provide a larger estimate of Hill number and almost equivalent estimate of species richness, as smaller plots (Fig. 3). Current available large plot floristics data are limited to these three sites and therefore preclude speculation about why this may be the case at BCI. Nevertheless, this finding provides a caution to interpretations among different plot methods across different tropical forests in larger meta-analyses.

A second limitation to our study is that forest properties related to the ecosystem services of carbon storage and sequestration clearly encompass more than simple estimates of tree AGB. Estimates of carbon stocks in other vegetation, coarse woody debris (CWD) and soil carbon pools are required in addition to AGB estimates for trees. Soil carbon and CWD parameters can also easily be integrated into plot methods, as CWD is often estimated using interception methods along linear transects at least 250 m in length (Harmon & Sexton 1996). Such transects could be arranged across any plot type, for example centered along the base transect of Gentry plots to integrate measures of CWD and AGB. Appropriate estimates of soil carbon pools can be assessed by modifications of any soil sampling protocol that accompanies a particular plot method (*e.g.*, Fisher *et al.* 2008).

Before making a decision on the most appropriate method for use in a given situation, our results should be integrated with other criteria. First, before adopting a specific protocol it is wise to consider the ability of any proposed method to compare with other existing networks of plot inventories in other sites. The two most common methods in the Neotropics include 1 ha plots, which number more than 1000 (Stropp *et al.* 2009; H. ter Steege, unpubl. data) and 0.1 ha Gentry plots, of which there are currently more than 800 (Phillips *et al.* 2003; Stegen *et al.* 2011; Table 1). The 1 ha plots thus remain a valuable option where resources are less limited, as they permit comparisons with plots including those managed by the RAINFOR consortium (*e.g.* Phillips *et al.* 2009). One hectare plots may be suboptimal for any individual purpose, such as estimates of AGB or tree diversity as we found in this study, but they have proven to be a tested compromise to address multiple questions/purposes that can shift and expand with time.

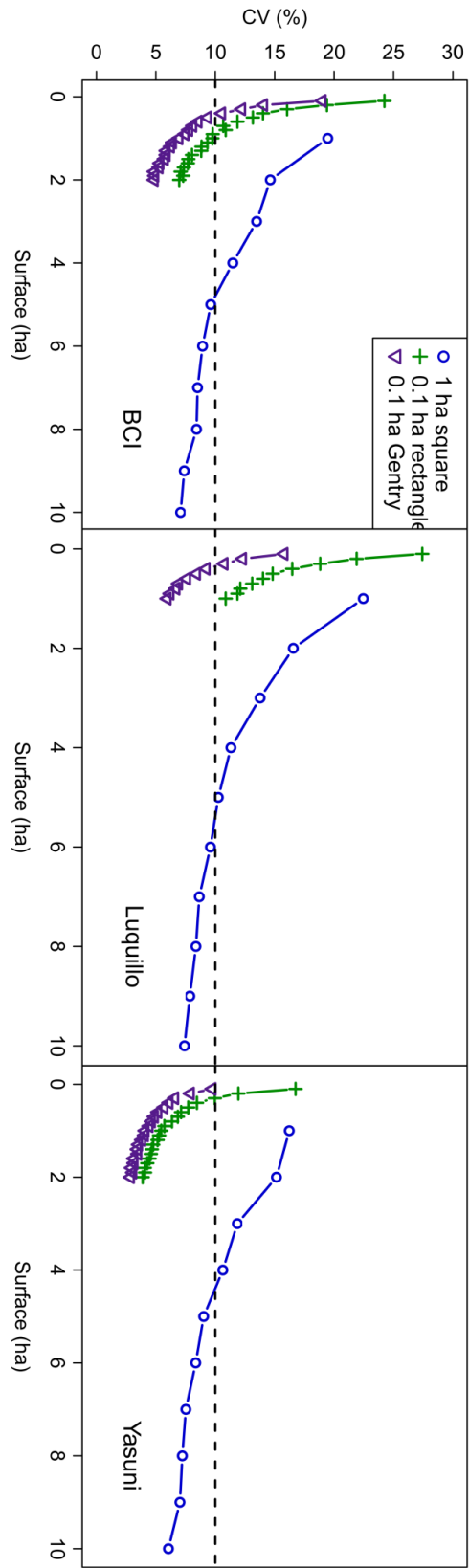


FIGURE 4. The relative precision (CV) of three plot methods for estimating tree diversity (Hill number) across three Neotropical forests. Each point represents 1000 simulations of each plot method in each forest site. Reference lines indicate an accepted minimum precision at a CV of 10 percent. Note that the 1-ha plot method estimates tree diversity for stems ≥ 10 cm dbh, whereas the other two methods estimate diversity of stems ≥ 2.5 cm dbh. (*Color version available in online Supporting Information*).

We caution against the use of 0.1 ha Gentry plots to estimate AGB, as they can be subject to a large degree of error for a given site. Indeed, Phillips *et al.* (2006) and Stegen *et al.* (2011) report unlikely values up to 600 Mg C ha⁻¹ (~ 1200 Mg AGB ha⁻¹) using 0.1 ha Gentry plots; and we must question the rates of recovery of AGB reported by Letcher and Chazdon (2009) following pasture abandonment, as they used a small number of 0.1 ha Gentry plots that may have overestimated the contribution of sparsely-distributed larger trees. Instead, we suggest investing the marginal additional effort to expand these plots to the 0.5 ha modification, from which more accurate AGB estimates can be obtained while maintaining the ability to integrate floristic data with a large network of existing plots. To our knowledge, there are currently at least 140 0.5 ha modified Gentry plots established in Peru, Bolivia, Brazil, French Guiana, and Suriname (Baraloto *et al.* 2011).

We were not able to simulate the recently-developed cross-shaped aggregate plot method of the Brazilian National Forest Inventory due to its coverage area (4 ha) relative to the area of the datasets in our study (Table 2). However, we hypothesize that it would exhibit similar performance to the modified Gentry plot, with which it shares properties including aggregation of multiple transects across a large area and relative ease of implementation (Table 1). Given the lengthy discussions from which this method was constructed, and the plans of the Brazilian Forest Service for thousands of plots to be installed between 2012 and 2015 (D. Piotto, pers. comm.), this method merits further study and consideration.

A second important criterion when choosing an inventory method is the spatial heterogeneity of forest structure at the sampling site. One drawback of composite methods such as both the original and modified Gentry plots is that they risk overemphasizing the impact of different habitats across the landscape. In some cases this may be advantageous, such as when an overall estimate for a heterogeneous forest area is desired. If instead an estimate for a given forest type of limited dimensions, such as linear features including higher tributary floodplain forests or the *Guadua*-dominated forests of the southwestern Amazon is required, then finding a homogeneous and representative 200 × 100 m area for a modified Gentry plot may prove more difficult than a 100 × 100 m plot. In Yasuní, for example, valleys and ridges separated by less than 100 m within the permanent plot have markedly different floristic composition (Valencia *et al.* 2004).

One of the most important considerations for choosing an appropriate plot method is whether static (*e.g.*, AGB, basal area) or dynamic (*e.g.*, growth rates, mortality rates, biomass turnover rates) forest descriptors are a priority. Many of the rapid inventory techniques employing transects and smaller plots are not permanent, and thus do not allow easy re-censusing to measure temporal dynamics in floristics, species population dynamics, or forest structure (Foster *et al.* 1998). Even though the plot size for all of the methods we tested here has been suggested to be less than the ideal for accurate estimates of tree mortality and carbon flux in tropical forests (~4ha, Fisher *et al.* 2008,

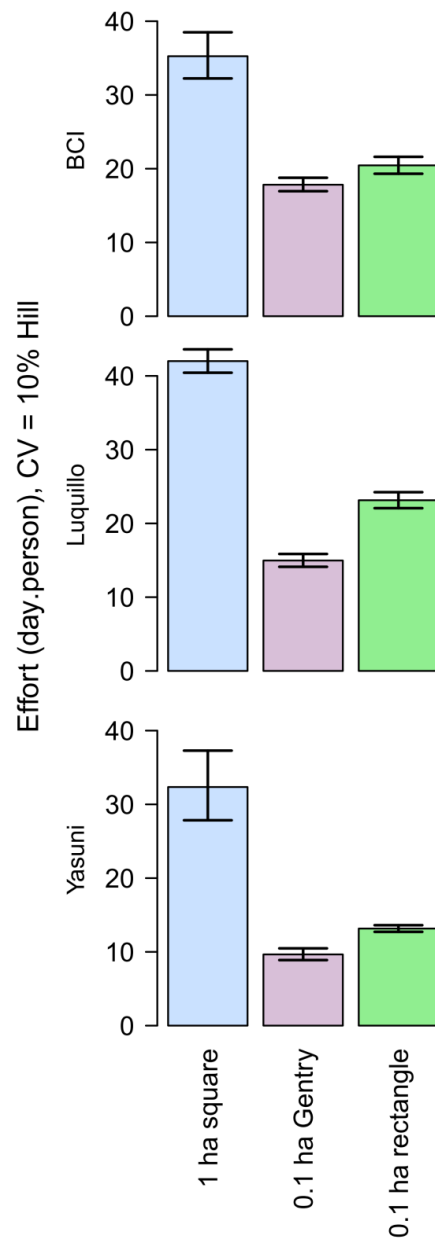


FIGURE 5. The sampling effort (in person days) required to achieve precise estimates of the Hill number for tree diversity (maximum of 10% CV) across three Neotropical forests using three different plot methods. Shown are the mean values (with 5 and 95% confidence intervals) of 1000 simulations of each plot method in each forest site.

Wagner *et al.* 2010), we believe that marking plots and trees in small plots remains a moderate and useful investment. This is particularly true in remote areas where the majority of resources are invested in transport rather than plot establishment; in this case permanent markings can permit subsequent measures of tree growth and survival and be linked to remote sensing analyses following changes in vegetation (Asner *et al.* 2010). Small plots will still be inadequate, however, to address interactions among tree species and the relative spatial and temporal dynamics in species' populations, community composition and the impact of human and natural disturbances.

We agree with Foster *et al.* (1998) and Hopkins (2007) who, when citing the current escalation in deforestation and forest degradation in tropical forests, have called for rapid inventories in areas that have been under-sampled. But we also believe that the results we present here suggest that such rapid inventories can be accomplished at least in part using plot methods that provide quantitative data useful to estimate both AGB and tree diversity. We propose that appropriate plot methods, together with information from *ad hoc* sampling (Foster *et al.* 2008), will assist in the identification and monitoring of forest areas to meet conservation priorities.

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REFERENCES

- ABRAHAMSON, I. L., C. R. NELSON, AND D. L. R. AFFLECK. Assessing the performance of sampling designs for measuring the abundance of understory plants. *Ecological Applications* 21: 452-464.
- ALDER, D. AND SYNNOTT, T. J. 1992. Permanent sample plot techniques for mixed tropical forests. Oxford Forestry Institute Tropical Forestry Paper 25, 124 pp.
- ASNER, G.P. & MARTIN, R.E. 2011. Canopy phylogenetic, chemical and spectral assembly in a lowland Amazonian forest. *New Phytologist* 189: 999-1012.
- ASNER, G.P., POWELL, G.V.N., MASCARO, J., KNAPP, D.E., CLARK, J.K., JACOBSON, J., KENNEDY-BOWDOIN, T., BALAJI, A., PAEZ-ACOSTA, G., VICTORIA, E., SECADA, L., VALQUI, M. & HUGHES, R.F. 2010. High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences* 107: 16738-16742.
- BACCINI, A., S. J. GOETZ, W. S. WALKER, N. T. LAPORTE, M. SUN, D. SULLA-MENASHE, J. HACKLER, P. S. A. BECK, R. DUBAYAH, M. A. FRIEDL, S. SAMANTA, AND R. A. HOUGHTON. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Clim. Change* 2: 182-185.
- BALTANAS, A. 1992. On the use of some methods for the estimation of species richness. *Oikos* 65: 484-492.
- BANKI, O. 2010. Does neutral theory explain community composition in Guiana Shield forests? PhD Dissertation, Utrecht University, the Netherlands.
- BARALOTO, C., RABAUD, S., MOLTO, Q., BLANC, L., FORTUNEL, C., DAVILA, N., MESONES, I., RIOS, M., VALDERRAMA, E. & FINE, P.V.A. 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology* 17: 2677-2688.
- BECK, J., AND W. SCHWANGART. 2010. Comparing measures of species diversity from incomplete inventories: an update. *Methods Ecol. Evol.* 1: 38-44.
- BOYLE BL 1996. Changes on altitudinal and latitudinal gradients in neotropical montane forests. St. Louis, MO: Washington University. 275 p.
- BROSE, U., N. D. MARTINEZ, AND R. J. WILLIAMS. 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology* 84: 2364-2377.
- CAMPBELL P, COMISKEY J, ALONSO A, DALLMEIER F, NUNEZ P, ET AL. 2002. Modified whittaker plots as an assessment and monitoring tool for vegetation in a lowland tropical rainforest. *Environmental Monitoring and Assessment* 76: 19-41.
- CHAMBERS JQ, NEGRÓN-JUÁREZ RI, HURTT GC, MARRA DM, HIGUCHI N 2009. Lack of intermediate-scale disturbance data prevents robust extrapolation of plot-level tree mortality rates for old-growth tropical forests. *Ecology Letters* 12: E22-E25.
- CHAVE J 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87-99.

- CHAVE J, COOMES D, JANSEN S, LEWIS SL, SWENSON NG, ET AL. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351-366.
- CONDIT R 1995. Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution* 10: 18-22.
- DE THOISY B, BROSSE S, DUBOIS M 2008. Assessment of large-vertebrate species richness and relative abundance in Neotropical forest using line-transect censuses: what is the minimal effort required? *Biodiversity and Conservation* 17: 2627-2644.
- EWERS, RM, G REYNOLDS, EC TURNER AND W. SINUN. 2010. The Stability of Altered Forest Ecosystems Project. Association for Tropical Biology and Conservation Annual Meeting, Bali, Indonesia.
- FAO 1981. Manual of forest inventory with special reference to mixed tropical forests. Rome, Italy: FAO.
- FEELEY, K.J. & SILMAN, M.R. 2011. The data void in modeling current and future distributions of tropical species. *Global Change Biology* 17: 626-630.
- FELDPAUSCH, T. R., L. BANIN, O. L. PHILLIPS, T. R. BAKER, S. L. LEWIS, C. A. QUESADA, K. AFFUMBAFFOE, E. J. M. M. ARETS, N. J. BERRY, M. BIRD, E. S. BRONDIZIO, P. DE CAMARGO, J. CHAVE, G. DJAGBLETEY, T. F. DOMINGUES, M. DRESCHER, P. M. FEARNSIDE, M. B. FRANÇA, N. M. FYLLAS, G. LOPEZ-GONZALEZ, A. HLADIK, N. HIGUCHI, M. O. HUNTER, Y. IIDA, K. A. SALIM, A. R. KASSIM, M. KELLER, J. KEMP, D. A. KING, J. C. LOVETT, B. S. MARIMON, B. H. MARIMON-JUNIOR, E. LENZA, A. R. MARSHALL, D. J. METCALFE, E. T. A. MITCHARD, E. F. MORAN, B. W. NELSON, R. NILUS, E. M. NOGUEIRA, M. PALACE, S. PATIÑO, K. S.-H. PEH, M. T. RAVENTOS, J. M. REITSMA, G. SAIZ, F. SCHRODT, B. SONKÅ, H. E. TAEDOUNG, S. TAN, L. WHITE, H. WÄLL, AND J. LLOYD. 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences* 8: 1081-1106.
- FISHER JI, HURTT GC, THOMAS RQ, CHAMBERS JQ 2008. Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecology Letters* 11: 554-563.
- FOSTER, R.B., HERNANDEZ, N.C., KAKUDIDI, E.K. & BURNHAM, R.J. 1998. Rapid assessment of tropical plant communities using variable transects: an informal and practical guide. Field Museum of Chicago. Chicago, Illinois.
- GARDNER TA, BARLOW J, ARAUJO IS, ÁVILA-PIRES TC, BONALDO AB, ET AL. 2008. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters* 11: 139-150.
- GASTON KJ 2000. Global patterns in biodiversity. *Nature* 405: 220-227.
- GENTRY AH 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* 15: 1-84.
- GORDON JE, NEWTON AC 2006. Efficient floristic inventory for the assessment of tropical tree diversity: A comparative test of four alternative approaches. *Forest Ecology and Management* 237: 564-573.

- GOTELLI N, COLWELL RK 2010. Estimating species richness. In: Magurran AE, McGill BJ, editors. *Biological diversity: Frontiers in measurement and assessment*. Oxford, UK: Oxford University Press.
- GULLISON RE, FRUMHOFF PC, CANADELL JG, FIELD CB, NEPSTAD DC, ET AL. 2007. Tropical forests and climate policy. *Science* 316: 985-986.
- HARMON, M. E., AND J. SEXTON. 1996. Guidelines for measurements of woody detritus in forest ecosystems. LTER Network Publication 20. University of Washington, Seattle.
- HOPKINS MJG 2007. Modelling the known and unknown plant biodiversity of the Amazon Basin. *Journal of Biogeography* 34: 1400-1411.
- HOUGHTON RA 2005. Aboveground forest biomass and the global carbon balance. *Global Change Biology* 11: 945-958.
- JOST L 2006. Entropy and diversity. *Oikos* 113: 363-375.
- LETCHER SG, CHAZDON RL 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in Northeastern Costa Rica. *Biotropica* 41: 608-617.
- LICHSTEIN, J. W., J. DUSHOFF, K. OGLE, A. CHEN, D. W. PURVES, J. P. CASPERSEN, AND S. W. PACALA. 2010. Unlocking the forest inventory data: relating individual tree performance to unmeasured environmental factors. *Ecological Applications* 20: 684-699.
- MAGURRAN AE, MCGILL BJ, EDITORS 2010. *Biological diversity: Frontiers in measurement and assessment*. Oxford, UK: Oxford University Press.
- MAGURRAN AE, QUEIROZ H. 2010. Evaluating tropical biodiversity: Do we need a more refined approach? *Biotropica* 42: 537-539.
- MALHI, Y., D. WOOD, T. R. BAKER, J. WRIGHT, O. L. PHILLIPS, T. COCHRANE, P. MEIR, J. CHAVE, S. ALMEIDA, L. ARROYO, N. HIGUCHI, T. J. KILLEEN, S. G. LAURANCE, W. F. LAURANCE, S. L. LEWIS, A. MONTEAGUDO, D. A. NEILL, P. N. VARGAS, N. C. A. PITMAN, C. A. QUESADA, R. SALOMAO, J. N. M. SILVA, A. T. LEZAMA, J. TERBORGH, R. V. MARTINEZ, AND B. VINCETI. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology* 12: 1107-1138.
- MALHI Y, ARAGÃO LEOC, METCALFE DB, PAIVA R, QUESADA CA, ET AL. 2009. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology* 15: 1255-1274.
- MYERS N, MITTERMEIER RA, MITTERMEIER CG, DA FONSECA GAB, KENT J 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- PHILLIPS OL, ARAGAO LEOC, LEWIS SL, FISHER JB, LLOYD J, ET AL. 2009. Drought Sensitivity of the Amazon Rainforest. *Science* 323: 1344-1347.
- PHILLIPS, OL, LAWRENCE, A., ISMODES, AR, LOPEZ, M., WOOD, D., ROSE, S., A. J. FARFAN. 2001. *Uma Metodologia De Evaluacion De La Biodiversidad Y De Los Recursos Del Bosque: Um*

- Manual Del Campo. Instituto De Investigaciones De La Amazonia Peruana, Puerto Maldonado, Peru.
- PHILLIPS OL, ROSE S, MENDOZA AM, VARGAS PN 2006. Resilience of southwestern Amazon forests to anthropogenic edge effects. *Conservation Biology* 20: 1698-1710.
- PHILLIPS OL, VARGAS PN, MONTEAGUDO AL, CRUZ AP, ZANS MEC, ET AL. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* 91: 757-775.
- PHILLIPS OL, VASQUEZ MARTINEZ R, NUNEZ VARGAS P, LORENZO MONTEAGUDO A, CHUSPE ZANS ME, ET AL. 2003. Efficient plot-based floristic assessment of tropical forests. *Journal of Tropical Ecology* 19: 629-645.
- PLOTKIN JB, POTTS MD, LESLIE N, MANOKARAN N, LAFRANKIE J, ET AL. 2000. Species-area curves, spatial aggregation, and habitat specialization in tropical forests. *Journal of Theoretical Biology* 207: 81-99.
- SAATCHI SS, HOUGHTON RA, DOS SANTOS ALVALA RC, SOARES JV, YU Y. 2007. Distribution of aboveground live biomass in the Amazon basin. *Global Change Biology* 13: 816-837.
- SAATCHI, S.S., HARRIS, N.L., BROWN, S., LEFSKY, M., MITCHARD, E.T.A., SALAS, W., ZUTTA, B.R., BUERMANN, W., LEWIS, S.L., HAGEN, S., PETROVA, S., WHITE, L., SILMAN, M. & MOREL, A. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences* 108: 9899-9904.
- SARMIENTO, C., S. PATIÑO, C. E. T. P. PAINE, J. BEAUCHENE, A. THIBAUT, AND C. BARALOTO. 2011. Within-individual variation of trunk and branch xylem density in tropical trees. *American Journal of Botany* 98: 1-10..
- SCHULZE CH, WALTERT M, KESSLER PJA, PITOPANG R, VEDDELER D, ET AL. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications* 14: 1321-1333.
- STEGEN JC, SWENSON NG, VALENCIA R, ENQUIST BJ, THOMPSON J 2009. Above-ground forest biomass is not consistently related to wood density in tropical forests. *Global Ecology and Biogeography* 18: 617-625.
- STEGEN, J.C., SWENSON, N.G., ENQUIST, B.J., WHITE, E.P., PHILLIPS, O.L., JØRGENSEN, P.M., WEISER, M.D., MONTEAGUDO MENDOZA, A. & NÚÑEZ VARGAS, P. 2011. Variation in above-ground forest biomass across broad climatic gradients. *Global Ecology and Biogeography* 20: 744-754.
- STROPP, J., TER STEEGE, H., MALHI, Y., ATDN & RAINFOR 2009. Disentangling regional and local tree diversity in the Amazon. *Ecography* 32: 46-54.
- VALENCIA R, FOSTER RB, VILLA G, CONDIT R, SVENNING JC, ET AL. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92: 214-229.

- VENTER O, LAURANCE WF, IWAMURA T, WILSON KA, FULLER RA, ET AL. 2009. Harnessing Carbon Payments to Protect Biodiversity. *Science* 326: 1368-.
- WAGNER F, RUTISHAUSER E, BLANC L, HERAULT B. 2010. Effects of plot size and census interval on descriptors of forest structure and dynamics. *Biotropica* 42: 664-671.
- WALTHER, B. A., AND J. L. MOORE. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 28: 815-829.

Chapitre 3

Propagation des incertitudes lors de l'estimation de la biomasse d'une parcelle inventoriée

Une fois l'inventaire d'une parcelle réalisé, la biomasse de chaque arbre peut être prédite. La somme des biomasses de tous les arbres d'une parcelle permet d'obtenir une biomasse forestière par unité de surface. Dans ce chapitre, nous définissons et analysons un modèle de biomasse à l'échelle de l'arbre.

Les variables prédictives de la masse d'un arbre sont son diamètre, sa hauteur, et sa densité de bois. Si les diamètres sont toujours mesurés, les hauteurs et des densités de bois doivent parfois être prédites et sont donc incertaines. Nous étudions l'impact de ces prédictions sur l'incertitude des estimations de biomasse. Les modèles sont calibrés avec des méthodes bayésiennes et les incertitudes sont propagées par les réalisations d'un processus de Monte-Carlo.

Les données de masse d'arbres contiennent 361 arbres qui ont été abattus et pesés en Guyane française en 1972. Contrairement à d'autres études, nous

modélisons la biomasse fraîche de ces arbres, car c'est la quantité qui a été mesurée. Pour la densité de bois, nous utilisons des mesures de gravité spécifique réalisées en Guyane française sur 2 504 arbres représentant 466 espèces. Le modèle de hauteur est calibré sur 1600 arbres mesurés en diamètre et en hauteur sur le site de Paracou.

Nous montrons que l'incertitude associée à une estimation de biomasse vient de l'incertitude de la relation entre la masse de l'arbre et les variables explicatives. L'incertitude sur ces dernières (hauteur, densité de bois) joue un rôle négligeable dans l'incertitude finale. L'incertitude sur les valeurs de densité de bois des arbres abattus fait que cette variable n'apparaît pas comme importante pour les prédictions de biomasse. En revanche, valeurs hauteurs biaisées entraînent un biais sur la valeur de la biomasse. Il est donc important d'avoir des valeurs de hauteur non biaisées, même incertaines.

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ERROR PROPAGATION IN BIOMASS ESTIMATION IN TROPICAL FORESTS

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ABSTRACT

1. Reliable above-ground biomass (AGB) estimates are required for studies of carbon fluxes and stocks. However, there is a huge lack of knowledge concerning the precision of AGB estimates and the sources of this uncertainty. At the tree level, the tree height is predicted using the tree diameter at breast height (DBH) and a height sub-model. The wood specific gravity (WSG) is predicted with taxonomic information and a WSG sub-model. The tree mass is predicted using the predicted height, the predicted WSG, and the biomass sub-model.

2. Our models were inferred with Bayesian methods and the uncertainty propagated with a Monte Carlo scheme. The uncertainties in the predictions of tree height, tree WSG, and tree mass were neglected sequentially to quantify their contributions to the uncertainty in AGB. The study was conducted in French Guiana where long-term research on forest ecosystems provided an outstanding data collection on tree height, tree dynamics, tree mass and species WSG.

3. We found that the uncertainty in the AGB estimates was found to derive primarily from the biomass sub-model. The models used to predict the tree heights and WSG contributed negligible uncertainty to the final estimate.

4. Considering our results, a poor knowledge of WSG and the height–diameter relationship does not increase the uncertainty in AGB estimates. However, it could lead to bias. Therefore, models and databases should be used with care.

5. This study provides a methodological framework that can be broadly used by foresters and plant ecologist. It provides the accurate confidence intervals associated with forest AGB estimates made from inventory data. When estimating region-scale AGB values (through spatial interpolation, spatial modelling, or satellite signal treatment), the uncertainty of the forest AGB value in the reference forest plots has to be taken in account. We believe that in the light of the Reducing Emissions from Deforestation and Degradation debate, our method is a crucial step in monitoring carbon stocks and their spatio-temporal evolution.

Keywords: Bayesian framework; uncertainty propagation; modelling; REDD

INTRODUCTION

Tropical forests are a large planetary carbon stock, with 40% of the Earth's total carbon stored in the terrestrial vegetation (from 158 to 324 Pg (Gibbs *et al.* 2007)). Tropical forests are also a dynamic stock for carbon through land-use change (emissions 1.3 ± 0.7 Pg yr⁻¹) and regrowth (1.6 ± 0.5 Pg yr⁻¹) (Pan *et al.* 2011). Preservation of this major carbon stock and the important role that forest ecosystems play in mitigating climate change are now fully recognized through the elaboration of mechanisms like Reducing Emissions from Deforestation and Degradation (REDD). An important challenge facing ecologists and foresters is to quantify as precisely as possible the carbon stocks and their fluxes at different spatial scales (Baker *et al.* 2010). However, considerable uncertainty about these figures remains.

Considerable efforts have recently been made to develop new tools to monitor tropical forest carbon stocks using an aerial approach (Goetz *et al.* 2009), together with new models of carbon estimation from tree measurements (Chave *et al.* 2005). Although uncertainty has been studied at the world scale (Pan *et al.* 2011; Saatchi *et al.* 2011), the uncertainty associated with tropical inventory data has rarely been explored (but see Chave *et al.* 2005). The above-ground biomass (AGB) of inventoried forest plots is estimated with tree-level models applied to forest inventory data. Exploring the uncertainty of AGB estimates made from tree data is essential for two reasons. First, uncertainty data are required to compare the spatial and temporal distributions of AGB. Second, the data obtained with aerial techniques must be calibrated against some reference inventory plots (Daniel *et al.* 2010; Dubois-Fernandez *et al.* 2010). Therefore, it is necessary to have unbiased AGB estimates for these plots and to quantify the uncertainties of these estimates. The AGB values in these reference inventory plots may have broad uncertainties. It is important to take this uncertainty in account when building spatial inference models. The 2000 IPCC (Intergovernmental Panel on Climate Change) report entitled “*Good Practice Guidance and Uncertainty Management in National Greenhouse Gas Inventories*” (IPCC 2000) points out the necessity of explicitly propagating uncertainties. In the paper, we provide a method to estimate AGB from inventory data while propagating uncertainty.

Inventory data consist of the diameters at breast height (DBHs) and some taxonomic information for all the trees in a precisely known area. Sometimes, tree heights are measured in the inventoried area or in part of it. Predicting the mass of a tree requires a physical model that roughly approximates the tree to a cone, which in turn requires that its DBH, height, and wood specific gravity (WSG) are known. The gap between the inventory data and the physical model is overcome by using three sub-models. The height sub-model predicts the height of a tree from its DBH. The WSG sub-model predicts the WSG of a tree from taxonomic information. The AGB sub-model predicts the mass

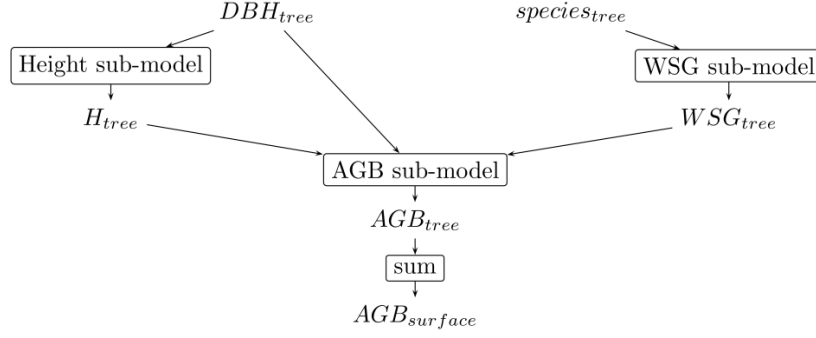


Figure 1. Biomass estimation process at the forest plot scale.

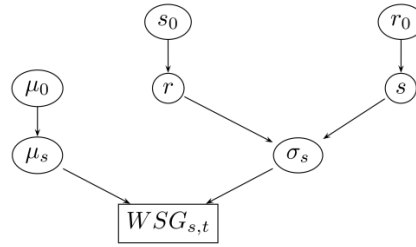


Figure 2. Directed acyclic graph of the wood specific gravity sub-model. $WSG_{s,t}$ is the wood specific gravity of tree t of species s ; μ_s is the mean parameter of species s ; σ_s is the variance parameter of species s . At a higher level, r and s are the parameters of the gamma distribution of all the σ_s values. μ_0 , s_0 , and r_0 are low-informative priors of their respective parameters.

of each tree using its DBH, height, and WSG (Fig. 1). The usual practice is to apply the three sub-models sequentially: the deterministic outputs of the height sub-model and the WSG sub-model are used as the inputs for the AGB sub-model.

These sub-models have already been examined (Chave *et al.* 2004; Feldpausch *et al.* 2011; Flores & Coomes 2011) in attempts to determine the best ones to apply in different cases. Chave *et al.* (2005) explored different sources of uncertainty in AGB estimates. However, past studies have focused on the sub-models themselves, assuming that the AGB model could be significantly improved with the improvement of its components. This assumption has yet to be studied by quantifying the parts of the AGB uncertainty that can be attributed to each sub-model.

We stress that the height sub-model, the WSG sub-model, and the AGB sub-model (sometimes called ‘AGB allometry’) must be integrated as the components of a unique AGB model. In the present study, we inferred the sub-model parameters with Bayesian numerical methods. The uncertainty contributed by the sub-models was propagated until the final AGB estimate was achieved.

The method is illustrated with data collected at Paracou, a long-established set of permanent plots in a moist tropical forest in French Guiana. A full set of data is available (WSG, tree girth, and height measurements) for this site and has already been used to estimate the carbon stocks and their fluxes in a natural forest (Rutishauser *et al.* 2010) and a logged forest (Blanc *et al.* 2009). This site was selected to provide feedback on the performances of P-band Synthetic Aperture Radar when it was used to measure the biomass and canopy height of a tropical forest with high-biomass stocks (Daniel *et al.* 2010; Dubois-Fernandez *et al.* 2010).

The objectives of this study were: 1) to propose a generic method that identifies the uncertainties associated with AGB estimates based on error propagation; 2) to apply this method to the French Guiana data; 3) to make practical recommendations to guide foresters and ecologists in producing the most precise AGB estimates.

MATERIAL AND METHODS

Data

All the data were collected in French Guiana. The climate of the region is equatorial, with two main seasons: a dry season from August to mid-November and a rainy season (often interrupted by a short drier period) from December to April (Gourlet-Fleury, Guehl & Laroussinie 2004).

Census data

The census data were for a 6.25 ha plot (plot 11) at the Paracou site in French Guiana (5°11'80"N, 52°12'30"W) (Gourlet-Fleury, Guehl & Laroussinie 2004). The site was established to study the responses to different logging intensities. In each plot, the diameter of trees (DBH) was measured at breast height (1.3 m) and above the buttresses if necessary. All stems with DBH > 10 cm were mapped, tagged, and measured biannually. In the present study, the biomass estimation method was applied to the unlogged inventory plots. We knew the diameter and some taxonomic information for each of the 3,992 trees. The DBHs ranged from 10 to 105 cm. Taxonomic information was available to the species level for 76% of the trees.

WSG data

The data were collected during the Bridge Project (Baraloto *et al.* 2010; Sarmiento *et al.* 2011). WSG is defined here as the mass (in grams) of an oven-dried sample divided by its green volume (in cm³) divided by the density of water (in grams per cm³) (Chave *et al.* 2006; Williamson & Wiemann 2010). The sample cores were 6 mm long, and therefore contained sapwood only. We do not assume these WSG measures to represent the WSG of the whole tree volume; we use them as statistical predictors of the tree AGB. The specific gravity of the sapwood had been measured for 2,504 trees in French Guiana, representing 466 species in 201 genera in 56 families. The number of measurements made for each species ranged from 1 (107 species) to 50 (*Lecythis persistens*); 100 species have eight or more measures.

Height data

We used data collected at the Paracou site. Height and DBH were measured in 1,603 trees. DBH ranged from 10 to 172 cm and height ranged from 4 to 47 m.

Mass data

The data were collected in 1972 during the ECEREX Project (Lescure *et al.* 1983). Three hundred and sixty-one trees were cut down on a 1 ha plot in French Guyana. The trees had been selected to include a range of diameters and heights. The mass, DBH, and height of each tree were measured along with some taxonomic information. The DBHs ranged from 5 to 118 cm, the heights from 2.7 to 47 m, and the masses from 3.6 kg to 25,500 kg. The biggest trees were not actually weighed but their masses were extrapolated from trunk, branches, and crown samples, and precise volumes (Lescure *et al.* 1983). The taxonomic information was known up to the species level (260 trees).

Sub-model definitions

Height sub-model

The role of the height sub-model is to predict the height of the trees from their diameters (Fig. 1). The height model is only used for biomass predictions. Measuring the heights of harvested trees presents no problem, although measuring standing trees does. Height-Diameter relationships have long been studied for temperate forest species (Huang, Titus & Wiens 1992). Because of the huge species richness, a species-specific height model would require huge, unavailable data sets to be inferred. Very few global height models have been published (Brown, Gillepsie & Lugo 1989; Feldpausch *et al.* 2011). After considering a Weibull model, Feldpausch *et al.* recommended the log-log model. After comparing four different model shapes (see Supplementary Material) we chose the Michaelis-Menten one: $\log(H_i) = \log(\alpha \cdot DBH_i / (\beta + DBH_i)) + \varepsilon_i$, $\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$, where ε represents the error of the model, assumed to be normally distributed. (Eqn. 1)

WSG sub-model (Fig. 2)

The role of the WSG model is to provide the WSG distribution for each tree, based on its species (Fig. 1). The WSG prediction is usually a deterministic call in a database. This is not appropriate in our study because our goal was to account for the variance in AGB. Our WSG sub-model explicitly accounts for the WSG variance within species. We assumed that for each species, the WSG has a truncated normal distribution. The distribution is truncated for physical realism so the wood density cannot be lower than 0.15 or higher than 1.3. The precision of the normal distribution follows a gamma distribution $G(r, s)$. At this level, the species were weighted by their numbers of measures. Species with a higher number of measures, and therefore a more reliable variance estimate, were given greater weight. This hierarchical structure based on the precision parameter allows meaningful estimates for species with very few measures.

In our predictions, the species of some trees was unknown or the species was not recorded in the WSG data set. Such trees were given a WSG distribution compiled from a mixture of the WSG distributions of all the known trees of the forest plot.

Biomass sub-model

The response variable was the fresh mass of the tree (kg). Different biomass models have been published and compared (Brown 1997; Araujo, Higuchi & Junior 1999; Chave *et al.* 2005). These models are generally built upon the mechanistic mass of a cylinder with the height, diameter, and WSG of the tree (Fig. 1), and some statistical corrections. The equation is log-transformed to achieve linearity. Some authors have chosen not to use these three predictive variables because tree height and WSG are difficult to obtain at the inventory scale (Ketterings *et al.* 2001; Chave *et al.* 2005; Pilli, Anfodillo & Carrer 2006). We preferred to include them all and deal explicitly with missing data. We

have given each variable its own coefficient to allow for any deviation from the mechanistic model: $\log(AGB_i) = \beta_0 + \beta_1 \log(DBH_i) + \beta_2 \log(H_i) + \beta_3 \log(WSG_i) + \varepsilon_i$, $\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$, where ε is the error term of the model, assumed to be normally distributed (Eqn. 2).

When inferring parameters $\beta_0, \beta_1, \beta_2, \beta_3$, and σ^2 , WSG_i is predicted from taxonomic information and is therefore uncertain. DBH_i , H_i , and the tree species are directly obtained from the harvested trees.

When predicting the biomass of standing trees, both WSG and height were predicted with their corresponding sub-models. DBH was measured and the species identified on the living trees.

Models inference

Bayesian methods

In the Bayesian paradigm, the parameter inference consists of updating the prior knowledge on the parameter from the data, generating the posterior distribution of the parameter. The parameter posterior distribution of the three models were inferred with numerical Bayesian methods (Monte Carlo Markov chain algorithms) (Gelman *et al.* 2003). These methods produce a sequence of values for each parameter, called a ‘chain’, which converges to the parameter posterior distribution. Once algorithm convergence is achieved, it is also said that the chain has reached its ‘stationary state’, and the values of the chain constitute a sample of the parameter posterior distribution.

The first iterations are discarded to ensure that the chain has reached the stationary state. Because the values of the chain could be correlated, we used a thinning procedure to produce a 1,000 quasi-independent samples from the posterior distribution of each parameter.

Height model

The parameters were estimated with Metropolis and Gibbs’ algorithm (Gelman *et al.* 2003).

WSG model

Two parameters were estimated for each species. The mean parameter μ_s has an improper prior. The variance parameter σ_s^2 follows a $IG(r, s)$ distribution. r and s have low-informative priors $\mathcal{N}_{[0, +\infty]}(0, 10^6)$. The posterior distributions of the parameters were estimated with the Metropolis–Hasting algorithm. The truncature introduced for physical reasons on the WSG distribution $\mathcal{N}_{[0.15, 1.3]}(\mu_s, \sigma_s^2)$ also helps the algorithm convergence by forcing him to explore physically realist values. Data were introduced sequentially, starting with the species with the highest weights (more than 10 measures). This helped the chains to reach their stationary states by avoiding some local

minima. After 5,000 iterations, the remaining data were introduced. Finally, for each parameter, we retained one value each for 70 of the last 70,000 iterations to reduce the autocorrelation between them. After this thinning, we obtained 1,000 quasi-independent samples of the posterior distributions of the parameters (Fig. 3). The algorithm details are given in Appendix 1.

Biomass model

The parameters of the AGB model were estimated with Gibbs' algorithm, using non-informative priors. For each tree in the mass data set, we generated 1,000 samples from the WSG posterior distributions of the WSG model parameters. At each step of Gibbs' algorithm, a sample from the WSG distribution for each tree was randomly chosen. See Appendix 3 for details of the algorithm.

Biomass prediction

The biomass of a tree was predicted with a Monte Carlo scheme from the posterior distribution of the model parameters. For each tree, we generated:

- 1,000 samples from its WSG distribution, using the WSG sub-model with parameters associated to the tree species. If the tree species is not known, the parameters are sampled from a mixture of the WSG distributions of all the trees in the forest plot. The truncature on $[0.15, 1.3]$ of the WSG distribution ensure that the sampled values are realistic.
- 1,000 samples from its height distribution, using the Height sub-model and its DBH.
- 1,000 samples from its AGB distribution, using the AGB sub-model its DBH and each sample from its WSG distribution, and its height distribution.

This protocol was applied to the 3,992 trees in the forest plot. Samples from the plot biomass distribution were obtained by summing the mass of each tree. This mass was converted into tonnes per hectare, the usual units. We can calculate any information from the predictive distribution of the plot biomass, such as the mean, quantiles, or credibility interval (Table 3).

Quantification of the error sources

The prediction of the AGB of the forest plot was based on three sub-models: the height sub-model, the WSG sub-model, and the AGB sub-model. These three sub-models were sources of uncertainty in the estimation of the plot AGB. To quantify the uncertainty each sub-model contributed to the AGB estimates, each was considered as deterministic, one at a time.

To consider a model deterministic, its parameters were replaced by their expected values computed from their chains as the mean of 1,000 values. We then examined the changes in the biomass prediction distributions, for both the trees and the forest plot (Table 3, Fig. 4).

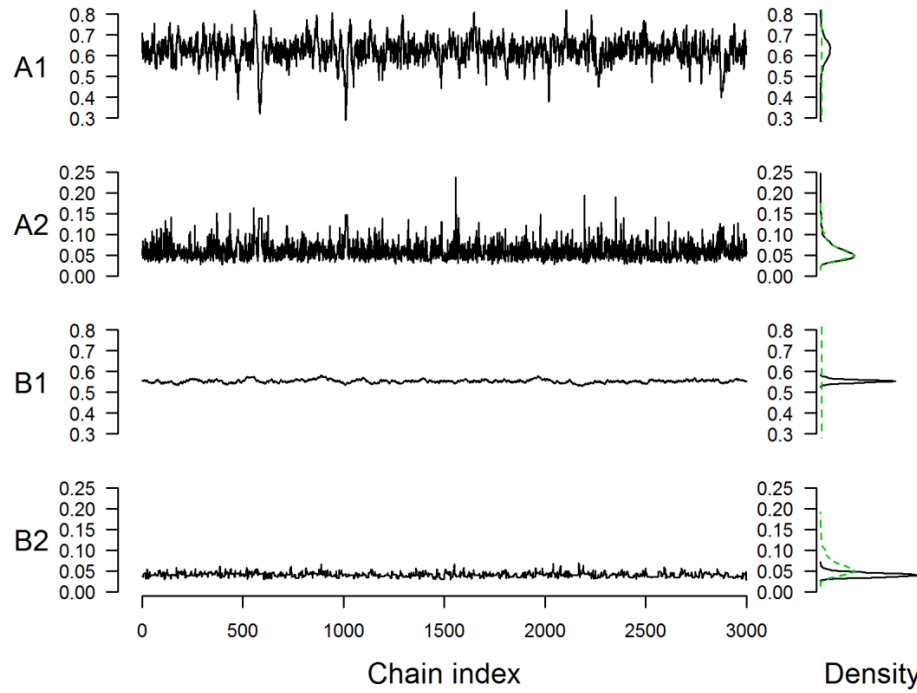


Figure 3. Posterior distributions of the WSG model parameters for two species, plus the WSG distribution simulated from these parameters. A: *Andira inermis* (one measure only); B: *Carapa procera* (27 measures): 1, mean parameter μ ; 2, variance parameter σ . Dashed line: prior distribution.

When a model is considered deterministic, the uncertainty it brings to the biomass estimate disappears. This causes the AGB uncertainty to decrease. We used this decrease to quantify the part of the AGB uncertainty that could be ascribed to that model.

RESULTS

Model parameter values

Height model

The height (Table 1) model was calibrated on a local data set and thus cannot be used for other tropical sites. Because many authors have found site and environmental effects in tree height modelling (Feldpausch *et al.* 2011; Lines *et al.* 2012), we believe that it is always better to use local models.

WSG model

The posterior distributions for μ_s (mean parameter) and σ_s (variance parameter) were sampled for the 463 species of the data set (Fig. 3). If the number of observations is low (e.g., *Andira inermis*, Fig. 3), the variance parameter distribution is the same as the hierarchical prior distribution. If the number of observations is high (e.g., *Andira inermis*, Fig. 3), the model allows deviations from the prior. As expected, the predicted WSG of each species was centred on the mean of the observed values.

AGB model

The posterior values of the AGB model coefficients are given in table 2. Under our conditions, the WSG signal was weak (coefficient value: 0.198). Previous studies have found WSG to be a key predictor of AGB at the tree level, or have chosen to fix the coefficient value to 1 for physical reasons (Chave *et al.* 2005). This difference is certainly attributable to the fact that WSG uncertainty was taken into account in inferring the AGB sub-model parameters.

The parameter posterior values (Table 2) were very close to Chave's values (Chave *et al.* 2005), especially the error parameter (Chave 2005: $RSE = 0.302$; present model: $1/\sqrt{\tau} = 0.323$).

AGB value

Using the previous models, we predicted the AGB for individual trees and for the forest plot (Table 3). The final biomass estimate for the forest plot was 451 Mg ha^{-1} , with a credibility interval of [441, 461]. This estimate is slightly higher than previous estimates (421 Mg ha^{-1} in 2007; (Chave *et al.* 2005; Goetz *et al.* 2009). We believe our estimate to be more accurate because we used local models only, rather than pan-tropical equations.

Parameter	Value
α	40.3 [38.8, 42.1]
β	9.43 [9.77, 9.68]
$\tau = 1/\sigma^2$	27.6 [24.6, 30.6]

Table 1. Posterior distributions of the height model parameters

$\log(H_i) \sim \log(\alpha \cdot DBH_i / \beta + DBH_i) + \varepsilon_i$, $\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$. Values are medians [95% Bayesian credibility intervals].

Parameter	Value
β_0	-2.91 [-3.12, -2.69]
β_1	2.19 [2.07, 2.31]
β_2	0.756 [0.604, 0.92]
β_3	0.187 [-0.0149, 0.381]
$\tau = 1/\sigma^2$	9.79 [8.31, 11.3]

Table 2. Posterior distributions of the biomass model parameters $\log(AGB_i) = \beta_0 +$

$\beta_1 \log(DBH_i) + \beta_2 \log(H_i) + \beta_3 \log(WSG_i) + \varepsilon_i$, $\varepsilon_i \sim \mathcal{N}(0, \sigma^2)$. Values are medians [95% Bayesian credibility intervals].

It should be noted that the AGB of a surface is the sum of the AGBs of the trees on that surface. Therefore, the variance in the AGB of the surface is the sum of the variances of the trees. As the surface increases, the variance increases as an absolute value in Mg, but decreases as a relative value in Mg ha^{-1} .

Identification of error sources

The AGB of the P11 plot at Paracou, with all error sources taken in account, was 451 Mg ha^{-1} . The Bayesian 95% credibility interval around this estimate had a range of 20 Mg ha^{-1} ($\pm 2.2\%$). This range was compared with the range of the credibility intervals of the AGB estimates when one sub-model was considered deterministic.

When the height model was considered deterministic, the credibility interval range was similar: 19 Mg ha^{-1} . Therefore, the height sub-model contributed no uncertainty to the AGB estimate.

When the WSG model was considered deterministic, the credibility interval range was also similar: 20 Mg ha^{-1} . Therefore, the WSG model contributed no uncertainty to the AGB estimate.

When the AGB sub-model was considered deterministic, the credibility interval range was narrower: 6 Mg ha^{-1} . Therefore, the AGB sub-model is the model that contributed the largest part of the uncertainty in the AGB estimate.

DISCUSSION

Error propagation

Using a statistical model for prediction makes that prediction uncertain. This uncertainty has different sources:

- Measurement error. When collecting data, measurements are more or less repeatable. The distribution of repeated measures around a “true value” is the measurement error. When a measured variable is used to infer a model, this error is part of the error term of the model. We did not quantify the part of the error model that derived from the measurement error, but a previous study found it to be negligible (Chave *et al.* 2004).

- Prediction error. When a model is used for prediction, the predicted values are uncertain. This uncertainty comes from: 1) the model itself, through its error term and the uncertainty of its parameters; and 2) the uncertainty of the other variables used in the model. These prediction errors are our great concern because they are often disregarded. Whereas it is quite natural to propagate these uncertainties in a Monte Carlo environment, the process usually makes the computation more complex (but not impossible; see for example (Gourlet-Fleury *et al.* 2011)). The IPCC recommend the use of the Monte-Carlo scheme when required (IPCC 2000).

AGB (kg for single trees, Mg ha ⁻¹ for the plot)							
Species	DBH	Height	WSG	All error sources	Height model deterministic	WSG model deterministic	AGB model deterministic
Treel	Eperua falcata	20.2	18.9 [11.3, 26.2]	0.637 [0.545, 0.728]	334 [160, 660]	337 [182, 624]	339 [156, 662]
Treel	unknown	20.0	18.9 [11.2, 26.1]	0.691 [0.429, 0.888]	329 [160, 653]	333 [175, 637]	334 [161, 686]
Treel	Eperua grandiflora	82.1	32.5 [24.8, 40.4]	0.679 [0.567, 0.788]	11100 [5590, 21100]	11300 [6040, 21400]	11100 [5970, 21100]
Plot P11				451 [441, 461]	452 [443, 462]	452 [442, 462]	451 [448, 454]

Table 3. Estimates of AGB and descriptors for three trees (AGB in kg) and for the entire plot P11 (AGB in Mg ha⁻¹). Each estimator is presented with its median and its 95% Bayesian credibility interval in brackets.

% of biais		-10%	-5%	-2%	+2%	+5%	+10%
Variable							
DBH		-20.6 [-19.7, -21.6]	-10.6 [-10.1, -11.2]	-4.33 [-4.12, -4.57]	4.44 [4.21, 4.69]	11.3 [10.7, 12]	23.2 [21.9, 24.7]
Height		-7.63 [-5.97, -9.14]	-3.79 [-2.95, -4.56]	-1.51 [-1.17, -1.82]	1.5 [1.16, 1.82]	3.74 [2.89, 4.54]	7.44 [5.73, 9.06]
WSG		-1.94 [0.313, -4.05]	-0.949 [0.152, -1.99]	-0.375 [0.0599, -0.79]	0.369 [-0.0587, 0.78]	0.911 [-0.145, 1.93]	1.79 [-0.282, 3.81]

Table 4. Percent of bias in AGB for three possible bias in the predictive variables DBH, H, and WSG. 95% confidence intervals are indicated in brackets

Here, we identified the AGB sub-model as the main source of error in the prediction of AGB, but we did not explore the uncertainty sources inside it: measurement errors or the natural diversity among the trees. However, because measuring harvested trees is not difficult, we can hypothesize that the measurement error is only a tiny part of the AGB sub-model error.

Consequences and recommendations

On variance

When focusing on the precision of AGB estimation, it is unnecessary to improve the quality of the WSG or height sub-models. The actual basic models are precise enough compared with the AGB sub-model.

The only way to improve the precision of the AGB predictions is to improve the precision of the AGB sub-model. Adding more trees to the calibration data may be a way to improve the precision of the model. However, there will always be diversity in AGB among trees of the same height, DBH, and WSG. Because our error term in the AGB model is the same as those found previously for large data sets (Chave 2005: $RSE = 0.302$; present model: $1/\sqrt{\tau} = 0.323$), we strongly believe that we had already reached the limit.

Another way to improve the precision of the AGB predictions could be to change the AGB sub-model, adding new variables to explain the residual variance. Variables that extend our knowledge of the tree volume (such as trunk taper, diameters at various heights, crown size, etc.) or tree density (WSG measured along the trunk, at all depths, etc.) would increase the precision of the model. However, the AGB model is used on large inventory data sets. If it requires too much data to be measured in the field, it will not be useful.

Bias introduced by the sampling strategy

First, the trees used to infer the model parameters must be representative of the trees whose AGB, height, and WSG are to be predicted. For this reason, we used only local data sets. Our models work best around the site at Paracou, where the height and weight data were collected. This point has already been addressed (Chave *et al.* 2005; Goetz *et al.* 2009), but has not been identified as a source of bias.

Second, models should never be used outside their domains of definition. This happens when, for example, we predict the height of a tree with a higher DBH than any tree in the height calibration data set. Because the behaviour of the model outside its range of definition has not been calibrated against the data, predictions outside this range may be biased. This can be corrected by extending the range of the calibration data sets. Measuring the heights and weights of the largest trees should make us more confident of the mass predictions for very large trees.

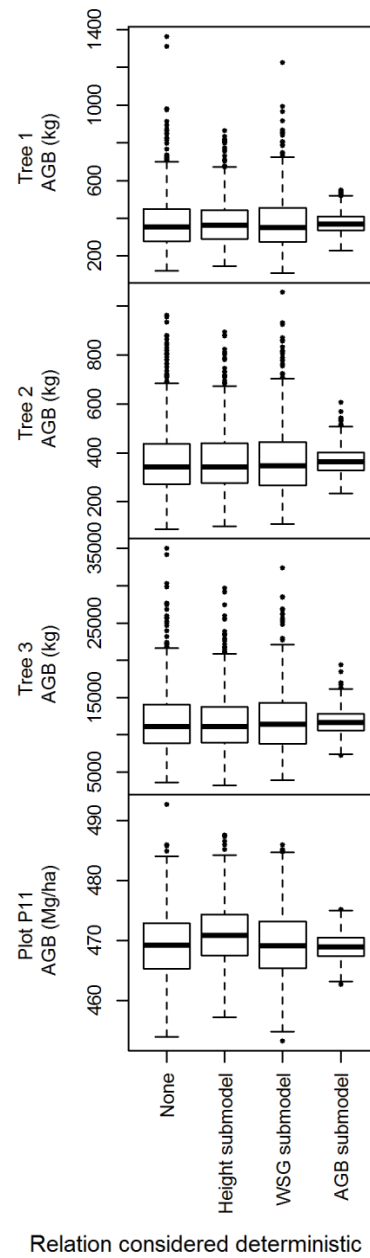


Figure 4. Boxplot of the AGB posterior distribution for three trees (described in Table 3) and for the 6.25 ha Paracou forest plot P11.

Bias from predictive variables

Bias is a deviation of the expected value of a variable from its definition. This definition is not a physical or biological definition, although it should be close. The definitions of the variables are chosen with the calibration data set. Once the models are inferred, the definitions of the variables must remain absolutely immutable.

If, during the prediction, a variable does not have the same expected value that it would have had in the calibration data set, it is biased. A biased variable at this stage creates bias in the AGB estimate. The bias p_{AGB} % in the AGB estimate induced by a bias of p_X % in the predictive variable X associated with a coefficient β_X can be calculated with the formula:

$$p_{AGB} = \left(\left(1 + \frac{p_X}{100} \right)^{\beta_X} - 1 \right) * 100$$

We calculated p_{AGB} for the three predictive variables (WSG, DBH, and H) and for six values of p_X (−10%, −5%, −2%, +2%, +5%, +10%). The results are given in Table 4.

Diameter: The DBH variable is the most standard variable in forest inventory data. In the AGB calibration data set, it is necessary to measure the diameter with respect to the inventory procedure. In this way, no bias can occur. DBH is the predictive variable that is most sensitive to bias (Table 4) because it has the highest coefficient (Table 2).

Height: In the AGB data set, height is easily measured after the tree is harvested. Therefore, this height definition is used in the biomass model, and this height must be the objective when height is measured in the field. Bias occurs if the height measured in the field differs from this definition. In Table 4, we see that a bias of 2%–5% in height creates a bias that can force the AGB estimate outside its confidence interval. A comparison of height measurements with different methods and on harvested trees should be enlightening.

WSG: In Table 4, we see that our model is not very sensitive to WSG bias. This derives from the low value of the coefficient (Table 2). Models with different coefficient values would have different sensitivities to WSG bias. For example, some authors fixed the WSG coefficient to one for physical reasons (Chave 2005). In this case, the bias induced in the AGB prediction was the same as the bias in WSG.

The definition of WSG and the measurement methods used have been widely discussed in the literature. A consensus seems to have emerged for WSG (oven-dried mass [72 h at 104 °C] divided by green volume). Other measurements can be converted to WSG with various formulae (Muller-Landau 2004; Chave *et al.* 2009).

The definition of “wood sample” is also contentious. It seems difficult to argue that one definition is better than another, but because there is evidence for large within-individual variations (Parolin 2002; Woodcock & Shier 2002; Williamson & Wiemann 2010), it seems a bad idea to mix different sampling methods.

Again, the most important point is consistency. The definition of a variable must remain the same in every data set, from the calibration of the model to its use in prediction. If necessary, variables can be corrected to avoid bias. Note that these corrections are additional models that can also contribute uncertainty.

CONCLUSION

In this paper, we have proposed a method to quantify uncertainty and identify its sources in biomass estimation. The most important source is the biomass sub-model, and the other sources are negligible. New height models or new WSG modelling methods, even if better than previous ones, will not necessarily improve the quality of carbon stock assessments. This study provides a methodological framework that can be broadly used by foresters and plant ecologists to provide accurate confidence intervals for tree biomass estimates from inventory data. This method can also be applied at the regional scale with error propagation. We believe that in the light of the REDD debate, such a method is a crucial step in accurately monitoring carbon stocks and their spatio-temporal evolution.

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REFERENCES

- Araujo, T.M., Higuchi, N. & Junior, J.A.D. (1999) Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Para, Brazil. *Forest Ecology and Management*, **117**, 43-52.
- Baker, D.J., Richards, G., Grainger, A., Gonzalez, P., Brown, S., DeFries, R., Held, A., Kellndorfer, J., Ndunda, P., Ojima, D., Skovseth, P.E., Souza, C. & Stolle, F. (2010) Achieving forest carbon information with higher certainty: A five-part plan. *Environmental Science & Policy*, **13**, 249-260.
- Baraloto, C., Paine, C.E.T., Patino, S., Bonal, D., Herault, B. & Chave, J. (2010) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, **24**, 208-216.
- Blanc, L., Echard, M., Herault, B., Bonal, D., Marcon, E., Chave, J. & Baraloto, C. (2009) Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecological Applications*, **19**, 1397-1404.
- Brown, S. (1997) Estimating biomass and biomass change of tropical forests: A Primer. *FAO Forestry Paper 134*, pp. 55. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
- Brown, S., Gillepsie, A.J.R. & Lugo, A.E. (1989) Biomass estimation methods for tropical forests with applications to forestry inventory data. *Forest Science*, **35**, 881-902.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87-99.
- Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 409-420.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351-366.
- Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Ter Steege, H. & Webb, C.O. (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, **16**, 2356-2367.
- Daniel, S., Dubois-Fernandez, P., Thuy Le, T., Chave, J., Blanc, L. & Davidson, M. (2010) P-band SAR study of tropical forest in French Guiana. *Remote Sensing for Agriculture, Ecosystems, and Hydrology Xii* (ed. C.M.U.M.A. Neale).
- Dubois-Fernandez, P., Oriot, H., Coulombeix, C., Cantalloube, H., du Plessis, O.R., Thuy Le, T., Daniel, S., Chave, J., Blanc, L., Davidson, M., Petit, M. & Ieee (2010) *TROPISAR: EXPLORING THE TEMPORAL BEHAVIOR OF P-BAND SAR DATA*.
- Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djangbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., Franca, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patino, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrod, F., Sonke, B., Taedoumg, H.E., Tan, S., White, L., Woll, H. & Lloyd, J. (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences*, **8**, 1081-1106.
- Flores, O. & Coomes, D.A. (2011) Estimating the wood density of species for carbon stock assessments. *Methods in Ecology and Evolution*, **2**, 214-220.
- Gelman, A., Carlin, J., Stern, H. & Rubin, D. (2003) *Bayesian Data Analysis, Second Edition* (Chapman & Hall/CRC Texts in Statistical Science). Chapman and Hall/CRC.
- Gibbs, H.K., Brown, S., Niles, J.O. & Foley, J.A. (2007) Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters*, **2**, -.

- Goetz, S.J., Baccini, A., Laporte, N.T., Johns, T., Walker, W., Kellndorfer, J., Houghton, R.A. & Sun, M. (2009) Mapping and monitoring carbon stocks with satellite observations: a comparison of methods. *Carbon balance and management*, **4**, 2.
- Gourlet-Fleury, S., Guehl, J.M.L. & Laroussinie, O. (2004) *Ecology and management of a neotropical rainforest - lessons drawn from Paracou, a long-term experimental research site in French Guiana*. Elsevier.
- Gourlet-Fleury, S., Rossi, V., Rejou-Mechain, M., Freycon, V., Fayolle, A., Saint-Andre, L., Cornu, G., Gerard, J., Sarrailh, J.-M., Flores, O., Baya, F., Billand, A., Fauvet, N., Gally, M., Henry, M., Hubert, D., Pasquier, A. & Picard, N. (2011) Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests. *Journal of Ecology*, **99**, 981-990.
- Huang, S.M., Titus, S.J. & Wiens, D.P. (1992) Comparison of Nonlinear Height Diameter Functions for Major Alberta Tree Species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **22**, 1297-1304.
- IPCC (2000) IPCC Good Practice Guidance and Uncertainty Management in National Greenhouse Gas Inventories. Hayama, Kanagawa, Japan.
- Ketterings, Q.M., Coe, R., van Noordwijk, M., Ambagau, Y. & Palm, C.A. (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management*, **146**, 199-209.
- Lescure, J.P., Puig, H., Riera, B., Leclerc, D., Beekman, A. & Beneteau, A. (1983) La phytomasse épigée d'une forêt dense en Guyane française. *Acta OEcologica*, **4**.
- Lines, E.R., Zavala, M.A., Purves, D.W. & Coomes, D.A. (2012) Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. *Global Ecology and Biogeography*.
- Muller-Landau, H.C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**, 20-32.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011) A Large and Persistent Carbon Sink in the World's Forests. *Science*.
- Parolin, P. (2002) Radial gradients in wood specific gravity in trees of Central Amazonian floodplains. *Iawa Journal*, **23**, 449-457.
- Pilli, R., Anfodillo, T. & Carrer, M. (2006) Towards a functional and simplified allometry for estimating forest biomass. *Forest Ecology and Management*, **237**, 583-593.
- Rutishauser, E., Wagner, F., Herault, B., Nicolini, E.A. & Blanc, L. (2010) Contrasting above-ground biomass balance in a Neotropical rain forest. *Journal of Vegetation Science*, **21**, 672-682.
- Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M. & Morel, A. (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 9899-9904.
- Sarmiento, C., Patino, S., Paine, C.E.T., Beauchene, J., Thibaut, A. & Baraloto, C. (2011) WITHIN-INDIVIDUAL VARIATION OF TRUNK AND BRANCH XYLEM DENSITY IN TROPICAL TREES. *American Journal of Botany*, **98**, 140-149.
- Williamson, G.B. & Wiemann, M.C. (2010) MEASURING WOOD SPECIFIC GRAVITY ... CORRECTLY. *American Journal of Botany*, **97**, 519-524.
- Woodcock, D.W. & Shier, A.D. (2002) Wood specific gravity and its radial variations: the many ways to make a tree. *Trees-Structure and Function*, **16**, 437-443.

Supplementary material

S1: height sub-model parameters inference

We consider the following model:

$$\log(H) \sim \mathcal{N}(\log(\mu), \sigma^2)$$

$$\mu = \frac{\alpha \cdot DBH}{\beta + DBH}$$

Set:

$$\tau = \frac{1}{\sigma^2}$$

Priors:

$$\begin{aligned} \alpha &\sim \mathcal{N}(\mu_{pri_\alpha}, \sigma_{pri_\alpha}^2) \\ \mu_{pri} &= 40, \quad \sigma_{pri}^2 = 10^6 \\ \beta &\sim \mathcal{N}(\mu_{pri_\beta}, \sigma_{pri_\beta}^2) \\ \mu_{pri} &= 20, \quad \sigma_{pri}^2 = 10^6 \\ \tau &\sim \mathcal{G}(r, s) \\ r &= 10^{-3}, \quad s = 10^{-3} \end{aligned}$$

The parameters posterior distributions are estimated with the Metropolis algorithm. At each step k, a new parameter value is sampled from the proposition distribution. The proposition is accepted with the probability p :

$$p = \frac{\mathcal{L}(\alpha^*, \beta^*, \sigma^*) \pi(\alpha^*, \beta^*, \sigma^*) p(\alpha^{k-1}, \beta^{k-1}, \sigma^{k-1} | \alpha^*, \beta^*, \sigma^*)}{\mathcal{L}(\alpha^{k-1}, \beta^{k-1}, \sigma^{k-1}) \pi(\alpha^{k-1}, \beta^{k-1}, \sigma^{k-1}) p(\alpha^*, \beta^*, \sigma^* | \alpha^{k-1}, \beta^{k-1}, \sigma^{k-1})}$$

where:

$\mathcal{L}(\alpha, \beta, \sigma) = \prod_{i=1}^n d\text{lnorm}(\log(H_i) | \mu, \sigma^2)$ is the likelihood,

$\pi(\alpha, \beta, \sigma) = d\text{norm}(\alpha | \mu_{pri_\alpha}, \sigma_{pri_\alpha}^2) \times d\text{norm}(\beta | \mu_{pri_\beta}, \sigma_{pri_\beta}^2) \times d\text{gamma}(\tau | r, s)$ is the prior, and

$p(\alpha^{k-1}, \beta^{k-1}, \sigma^{k-1} | \alpha^*, \beta^*, \sigma^*)$ is the probability of the preceding values given the new proposition in the proposition distribution.

Parameters are updated sequentially.

Metropolis algorithm: for $k=1$ to $k=100\,000$

Generate α and β from their proposition distribution

$$\alpha \sim \mathcal{N}_{[0, +\infty]}(\mu_{prop_\alpha}, \sigma_{prop_\alpha}^2)$$

$$\beta \sim \mathcal{N}_{[0,+\infty]}(\mu_{prop_\beta} \sigma_{prop_\beta}^2)$$

Accept or reject the proposition

Update τ :

$$\tau^k \sim \mathcal{G}\left(r + \frac{1}{2}n, s + \frac{1}{2}\sum_{i=1}^n (\log(H_i) - \log(\mu)^2)\right)$$

Discard a 10 000 iterations burn-in and keep 1 sample each 100 values of the chains.

S2: WSG sub-model parameters inference

The model parameters are estimated with the Metropolis algorithm. The proposition distribution is the Gibbs posterior distribution if the normal distributions were not truncated.

For each tree $i=1, \dots, n$ from species s in the WSG data we consider the following model :

$$WSG_i \sim \mathcal{N}_{[0.15,1.3]}(\mu_s, \sigma_s^2)$$

$$\tau_s \sim \mathcal{G}(r, s)$$

Set:

$$\tau_s = \frac{1}{\sigma_s^2}$$

Priors:

$$\mu_s \sim \mathcal{N}_{[0.15,1.3]}(\mu_{pri}, \sigma_{pri}^2)$$

$$\mu_{pri} = 0.5, \quad \sigma_{pri}^2 = 10^6$$

$$r \sim \mathcal{N}_{[0,+\infty]}(0, 10^6)$$

$$s \sim \mathcal{N}_{[0,+\infty]}(0, 10^6)$$

The parameters posterior distributions are estimated with the Metropolis algorithm. At each step k , a new parameter value is sampled from the proposition distribution. The proposition is accepted with the probability p :

$$p = \frac{\mathcal{L}(\mu_s^*, \sigma_s^*) \pi(\mu_s^*, \sigma_s^*) p(\mu_s^{k-1}, \sigma_s^{k-1} | \mu_s^*, \sigma_s^*)}{\mathcal{L}(\mu_s^{k-1}, \sigma_s^{k-1}) \pi(\mu_s^{k-1}, \sigma_s^{k-1}) p(\mu_s^*, \sigma_s^* | \mu_s^{k-1}, \sigma_s^{k-1})}$$

where :

$$\mathcal{L}(\mu_s, \sigma_s, r, s) = \prod_{s=1}^S d\text{gamma}(\tau_s | r, s) \times \prod_{i=1}^{n_s} d\text{tnorm}_{[0.15,1.3]}(WSG_i | \mu_s, \sigma_s^2) \text{ is the likelihood,}$$

$$\pi(\mu_s, \sigma_s) = dtnorm_{[0,+\infty]}(r|0, 10^6) \times dtnorm_{[0,+\infty]}(r|0, 10^6) \times \prod_{s=1}^S dtnorm_{[0.15,1.3]}(\mu_s|\mu_{pri}, \sigma_{pri}^2) \times dgamma(\tau_s|r_{pri}, s_{pri}) \text{ is the prior, and}$$

$p(\mu_s^{k-1}, \sigma_s^{k-1}, r^{k-1}, s^{k-1}|\mu_s^*, \sigma_s^*, r^*, s^*)$ is the probability of the preceding values given the new proposition generated with the proposition distribution.

Parameters are updated sequentially.

Metropolis algorithm: for $k=1$ to $k=100\,000$

Generate r et s from their proposition distribution

$$r^* \sim \mathcal{U}(\max(0, r^* - w), r^* + w)$$

$$s^* \sim \mathcal{U}(\max(0, s^* - w), s^* + w)$$

Accept or reject the proposition

For each species s

Generate μ_s^* and σ_s^* from their proposition distributions:

$$\mu_s^* \sim \mathcal{N}\left(\frac{\mu_{pri}\sigma_s^{k-1^2} + \sigma_{pri}^2 \sum_i WSG_{i,s}}{n_s \sigma_{pri}^2 + \sigma_s^{k-1^2}}, \frac{\sigma_s^{k-1^2} \sigma_{pri}^2}{n_s \sigma_{pri}^2 + \sigma_s^{k-1^2}}\right)$$

$$\tau_s^* \sim \mathcal{G}\left(s^{k-1} + \frac{n_s}{2}, r^{k-1} + \frac{\sum_i WSG_{i,s}^2}{2}\right)$$

Accept or reject the proposition

Discard a 10 000 iterations burn-in and keep 1 sample each 100 values of the chains.

S3: AGB sub-model parameters inference

For each tree $i=1, \dots, n$, we consider the following model :

$$\log(AGB_i) = \beta_0 + \beta_1 \log(DBH_i) + \beta_2 \log(H_i) + \beta_3 \log(WSG_i) + \varepsilon_i, \quad \varepsilon_i \sim \mathcal{N}(0, \sigma^2)$$

where AGB is the tree fresh mass, DBH the diameter at breast height, H the tree height, and WSG the tree wood specific gravity.

Set:

$$Y = \log(AGB_i)$$

$$\beta = [\beta_0, \beta_1, \beta_2, \beta_3] \text{ (Initial values)}$$

$$\Sigma = \sigma^2 I_4$$

$$\tau = \frac{1}{\sigma^2}$$

$$\Gamma = \tau * I_4$$

Priors:

$$\begin{aligned}\beta &\sim \mathcal{N}(\mathbf{M}_{pri}, \Sigma_{pri}^2) \\ \mathbf{M}_{pri} &= [0, 0, 0, 0], \quad \Sigma_{pri}^2 = 10^6 * I_4 \\ \tau &\sim \mathcal{G}(r_{pri}, s_{pri}) \\ r_{pri} &= 0.01, s_{pri} = 0.01\end{aligned}$$

Generate 1000 WSG values for each tree

Gibbs algorithm: for $k=1$ to $k=11000$

For each tree, pick a WSG sample at random: $WSG_{i,j,k}$

$$X = \begin{bmatrix} 1 \\ \vdots \\ DBH_{i,j} \quad H_{i,j} \quad WSG_{i,j,k} \\ 1 \end{bmatrix}$$

Update β from its marginal posterior distribution:

$$\beta^k \sim \mathcal{N}_4 \left(\left(X' \Gamma^{k-1} X + \Sigma_{pri}^{2^{-1}} \right)^{-1} \left(X' \Gamma^{k-1} Y + \Sigma_{pri}^{2^{-1}} \mathbf{M}_{pri} \right), \left(X' \Gamma^{k-1} X + \Sigma_{pri}^{2^{-1}} \right)^{-1} \right)$$

Update τ from its marginal posterior distribution:

$$\tau^k \sim \mathcal{G} \left(r_{pri} + \frac{1}{2} n, s_{pri} + \frac{1}{2} \sum_{i=1}^n (Y_i - \beta^k X_i)^2 \right)$$

Discard a 1 000 iterations burn-in and keep 1 sample each 10 values of the chains.

S4: Diameter-Height model shape selection

To choose the height-diameter model shape, we went through the following model selection procedure. The height-diameter data were collected on nine 1ha plots distributed along the northern part of French Guiana. The four candidate models are calibrated using a mix of Metropolis and Gibbs algorithm. Since all the models have the same number of parameters and were calibrated on the same data, we compared them with the criteria of the maximum value taken by the likelihood chain. H is the tree height, DBH is the tree diameter, α and β are the model coefficients, and ε is the error of the model, assumed normal with a variance of σ^2 .

Shapes considered:

Log-linear: $\log(H) \sim \log(\alpha + \beta \log(DBH)) + \varepsilon$

Log-log: $\log(H) \sim \alpha + \beta \log(DBH) + \varepsilon$

$$\text{Michaelis-Menten: } \log(H) \sim \log\left(\frac{\alpha DBH}{\beta + DBH}\right) + \varepsilon$$

$$\text{Weibull: } \log(H) \sim \log(\alpha (1 - \exp(-\beta DBH))) + \varepsilon$$

In the table A1 the model with the highest likelihood is colored. The Michaelis-Menten shape had more often the highest likelihood value. We then selected the Michaelis-Menten shape for modeling the height-diameter relation. Figure A2 shows how the model selected fits the data.

Plot	Log-linear	Log-log	Michaelis	Weibull
1	-1222,20	-1232,62	-1206,85	-1218,27
2	-1278,75	-1285,21	-1278,07	-1285,24
3	-1851,33	-1861,45	-1845,46	-1856,77
4	-1443,16	-1460,08	-1433,16	-1450,72
5	-1416,38	-1426,61	-1417,58	-1424,99
6	-1482,77	-1492,39	-1483,83	-1491,77
7	-1925,72	-1935,45	-1903,83	-1917,27
8	-1376,51	-1381,13	-1382,43	-1384,23
9	-1250,71	-1262,44	-1234,47	-1248,70

Table A1: Maximum likelihood for four height models on 9 sites in French Guiana. The colored cell indicates the model with the highest likelihood.

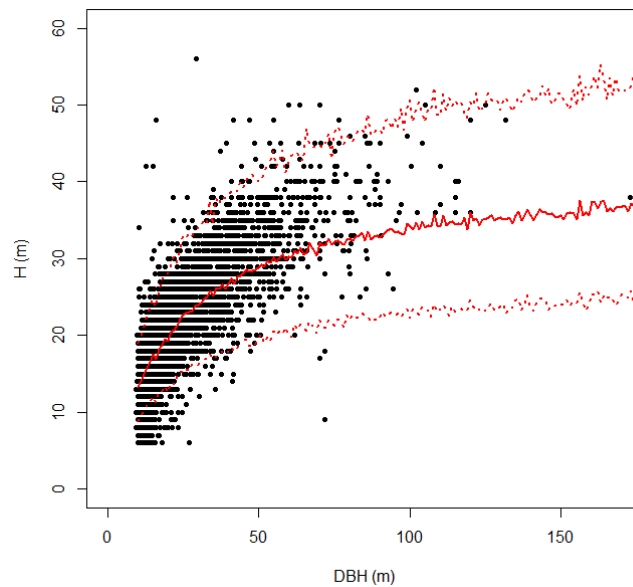


Figure A1: Height-diameter relationship. Each black point is a tree from the Height dataset. The plain (respectively dotted) red lines are the median (respectively 95% credibility interval) of the predicted heights with the Michaelis-Menten shape.

Chapitre 4

Modélisation de la relation diamètre-hauteur pour l'estimation de la biomasse

Dans le chapitre précédent, nous avons montré que la hauteur des arbres était une variable importante pour les prédictions de biomasse. Dans les inventaires forestiers, la mesure des hauteurs des arbres est rarement effectuée car elle demande un effort supplémentaire important. Pour prédire la biomasse, la hauteur de chaque arbre doit alors être prédite par un modèle reliant la hauteur d'un arbre à son diamètre.

Dans ce chapitre, nous comparons quatre formes de modèles hauteur-diamètre sur 42 parcelles en Guyane française (modèles log-linéaire, log-log, Weibull simplifié, Michaelis-Menten). Une fois la forme choisie, nous étudions la variabilité de la relation hauteur-diamètre entre les différents sites d'inventaires. Nous essayons d'expliquer cette variabilité en reliant les coefficients du modèle de hauteur à des variables décrivant la structure et l'environnement du peuplement forestier. Les

performances de chaque modèle sont évaluées sur leur capacité à remplacer les hauteurs mesurées pour la prédiction de la biomasse des parcelles.

Nous montrons que le modèle dit de Michaelis-Menten est bien adapté aux prédictions de hauteurs en forêt tropicale. La structure diamétrique du peuplement est un bon prédicteur des coefficients du modèle. Nous avons interprété la structure du peuplement comme un indice de maturité de la forêt : les peuplements plus jeunes et plus dynamiques, avec de nombreux arbres entre 10cm et 20cm de diamètre, sont très élancés mais avec une hauteur maximale faible. Les peuplements les plus vieux, avec un faible nombre de petits arbres, ont des arbres très hauts mais moins élancés.

Les variables d'environnement améliorent le modèle de hauteur mais de manière trop faible pour améliorer de façon significative les estimations de biomasse. Les variables environnementales n'expliquent pas de variabilité des relations hauteur-diamètre qui n'aurait pas été expliquée par les variables de structure diamétrique du peuplement.

PREDICTING TREE HEIGHT FOR BIOMASS ESTIMATES IN TROPICAL FORESTS

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ABSTRACT

The recent development of REDD+ mechanisms require reliable estimation of carbon stocks, especially in tropical forests that are particularly threatened by global changes. Even if tree height is a crucial variable to compute the above-ground forest biomass, tree heights are rarely measured in large-scale forest census because it requires consequent extra-effort. Tree height have thus to be predicted thanks to height models.

Height and diameter of all trees above 10 cm of diameter were measured in thirty-three half-ha plots and nine one-ha plots throughout the northern French Guiana, an area with substantial climate and environmental gradients. We compared four different model shapes and found that the Michaelis-Menten shape was the most appropriate for the tree biomass prediction. Model parameter's values were significantly different from one forest plot to another and neglecting these differences would lead to large errors in biomass estimates.

Variables from the forest stand structure explained a sufficient part of the plot-to-plot variations of the height model parameters to affect the AGB predictions. In the forest stands dominated by small trees, the trees were found to have rapid height growth for small diameters. In forest stands dominated by larger trees, the trees were found to have the greatest heights for large diameters.

The above-ground biomass estimation uncertainty of the forest plots was reduced by the use of the forest structure-based height model. It demonstrates the feasibility and the importance of height modeling in tropical forest for carbon mapping.

Tree height is definitely an important variable for AGB estimations. When the tree heights are not measured in an inventory, they can be predicted with a height-diameter model. This model can account for plot-to plot variations in height-diameter relationship thank to variables describing the plots. The variables describing the stand structure of the plots are efficient for this. We found that variables describing the plot environment (rainfall, topography...) do not improve the model much.

INTRODUCTION

Tropical forests are an important and dynamic stock of carbon on earth: they account for 40% of the carbon stored in the earth vegetation (Gibbs *et al.* 2007). Accurate estimates of Above-Ground Biomass (AGB) for tropical forests are needed to assess the spatial and temporal variation of these carbon stocks (Houghton *et al.* 2001). The AGB estimations have direct applications to forest management in the light of the recent developments of the carbon market and REDD+ (IPCC 2000; Gibbs *et al.* 2007).

Though considerable groundwork is being done, models used to predict biomass are often rough and need further improvements to lower biases and uncertainties (Houghton *et al.* 2001; Chave *et al.* 2005). Nowadays, AGB spatial extrapolation methods mostly rely on remote sensing data (Asner *et al.* 2010; Saatchi *et al.* 2011; Baccini *et al.* 2012). While very promising, these methods still require calibration points from well-known forest plot inventories (Lucas *et al.* 2002).

Forest census plots typically consist of various measurements of properties of all individual trees encountered on a given surface. Diameters at Breast Height (DBH) are always measured, generally starting at 10 cm. Depending on the inventory effort, additional information such as tree's height or species identity may be recorded. The AGB of a forest plot is the sum of the AGB of the trees belonging to this plot.

Tree AGB models use biological variables describing a tree to predict its individual AGB (Brown, Gillepsie & Lugo 1989; Brown 1997; Araujo, Higuchi & Junior 1999). The best models use the tree DBH, the tree height, and the tree wood density (Wood Specific Gravity, WSG) to catch the variability of tree biomass (Chave *et al.* 2005). Among these variables, the DBH is measured in the field and the effect of WSG is unclear for some authors (Molto, Rossi & Blanc in press).

Thus, for AGB prediction, tree height is a key variable that is generally not measured. It thus has to be predicted. In boreal forests, classical height models predict a tree height from its DBH for a given species (Sharma & Parton 2007). However, the biodiversity of tropical regions prevents the use of height models that include a species effect. In the past, various height-DBH model shapes have been proposed (Huang, Titus & Wiens 1992) but their applications to large scale tropical forests are rare (Brown, Gillepsie & Lugo 1989; Feldpausch *et al.* 2011).

The general objective of the paper is to explore the possibility to include additional information, such as structure and environmental variables, into the height-DBH model in order to build a flexible model that can be used for AGB estimations in different landscape context. To do thus, we used a dataset from French Guiana, consisting of 42 forest plots. These plot inventories are suitable for AGB assessments (IPCC 2000): DBH measured above 10 cm, height measures, species identification. The plots are situated in the northern part of French Guiana and were chosen to represent the contrasted

landscape of the region (Ferry *et al.* 2010; Baraloto *et al.* 2011; Gond *et al.* 2011). More specifically, we asked the following questions:

- 1- Which Height-DBH model shape is both robust and convenient to use?
- 2- Do the Height-DBH model parameters vary between sites? If true, do these variations affect the AGB predictions?
- 3- Can the forest plot stand structures and forest local environment explain the variability of the height-DBH model coefficients?

To reach the objective of setting a height-DBH model for AGB predictions, height models are evaluated on their ability to replace measured heights in the forest plot for AGB predictions. We use a tree AGB model set in French Guiana. The AGB model uses tree height, tree DBH, and tree WSG to predict tree fresh AGB. It allow for uncertainty from height and WSG predictions propagation through a Monte-Carlo sampling process (Molto, Rossi & Blanc in press). To evaluate the performance of a height-DBH model, we predict the AGBs of the trees using 1-measured heights and 2-predicted heights. The degradation of the precision of the AGB prediction between 1- and 2- gives us a measure of the performance of the height-DBH model.

MATERIAL AND METHODS

French Guiana

The study was conducted in French Guiana. The climate of the region is equatorial, with two main seasons: a dry season from August to mid-November and a rainy season (often interrupted by a short drier period in March) from December to April (Wagner *et al.* 2011). The relief comprises a hill system within a dense hydrographic network. Rainforests cover almost all the study area.

Forest plots

Inventory data came from two projects recently conducted in French Guiana. Description of the forest plots is available in the supplementary materials S2.

1- Inventories from the AMALIN project (Baraloto *et al.* 2011): 33 plot spread in various landscapes and topographical contexts (ridges, plateau, and lowlands). DBHs and tree heights were measured by a team of trained experts. The plots are divided in 2 subplots (details in (Baraloto *et al.* 2011) and represent a 0.1 hectare area (trees with DBH>10cm) nested in a 0.5 hectare area (trees with DBH>20cm).

2- Inventories from the BRIDGE project (Baraloto *et al.* 2010a): 9 one-hectare plots where trees with DBH>10 were measured for DBHs and heights. Heights were measured with various methods, mainly lasers and ropes when climbers could approach the top of the trees. The different methods were compared on field and showed very consistent estimates.

Forest plots descriptors

Descriptors of the forest structure

We chose variables commonly used by foresters to describe the stand DBH structure: the basal area (in m² per hectare) and the relative frequencies of four classes of stem size (between 10cm and 20cm, 20cm and 40cm, 40cm and 60cm, and above 60cm). To avoid mathematical singularity, the proportion of stems between 20 and 40 cm was discarded from the data. These descriptors were computed from DBHs measurements only and thus are always available in standard forest inventories.

Descriptors of the environment

We chose to work with mainstream, widely available environmental variables.

Four of these were computed from a Digital Terrain Model (DTM) with 90m-sided squared cells (NASA SRTM (USGS 2004)). (i) The drained area measures the surface of the hydraulic basin that flows through a cell. A low value indicates cells located close to the limit of two basins, whereas the highest values indicate cells located downstream. (ii) The hydraulic altitude was computed from the 3rd order hydraulic system. The hydraulic altitude of a cell is its altitude above the closest stream of its hydraulic basin. Lowest values (including 0), indicate that the forest plot is located in a potentially

temporarily flooded area while the highest values indicate that the forest plot is located at a top-hill area. (iii) The slope of each cell was computed with a 180 meters lag (2 cells). (iv) The Terrain Ruggedness Index (TRI) was computed with a 20 cells lag (1800 meters) to catch the difference between flat and more mountainous landscapes.

Two environmental variables were computed from the NASA TRMM rainfall data. One was the annual average rainfall in the ten last years (in mm); the other was a dry season index (DSI), computed as the average number of months with a rainfall below 100 mm (Wagner *et al.* 2012). The dry season index quantifies the length of the annual hydraulic stress for trees.

All maps and geographical information were computed with SAGA (Bock *et al.* 2004).

Height-DBH model shapes

M1 (Log-linear, eqn. 1): This height-DBH model has already been used for height-DBH modeling (Nogueira *et al.* 2008). Classically the error term was additive Normal, but we used a multiplicative Log-Normal to better address heteroscedasticity. The model may give negatives values for DBH lower than 1, but this is not a problem since the DBH are larger than 10 in standard forest inventories. The model has no horizontal asymptote for large values of DBH but thanks to the *log* function, the increase for large DBH values is extremely slow.

$$H_i = (\alpha + \beta \times \log(DBH_i)) \times \varepsilon_i, \quad \varepsilon_i \sim LN(0, \sigma^2) \quad \text{Eqn. 1}$$

M2 (Log-log, eqn. 2): This model is very frequently used in forest ecology (Brown, Gillepsie & Lugo 1989; Feldpausch *et al.* 2011). However, the existence of factors limiting the tree growth in height but not in DBH may question its basic assumptions. Indeed, this model is known for overshooting the height of the large trees (Feldpausch *et al.* 2011).

$$H_i = \exp(\alpha + \beta \times \log(DBH_i)) \times \varepsilon_i, \quad \varepsilon_i \sim LN(0, \sigma^2) \quad \text{Eqn. 2}$$

M3 (simplified Weibull, eqn. 3): This non-linear model is common in height-DBH relationship modeling (Fang & Bailey 1998; Feldpausch *et al.* 2011). Its shape presents an oblique asymptote with slope α/β at (0, 0) and a horizontal asymptote $H = \alpha$ when DBH is large.

$$H_i = \alpha \times \left(1 - \exp\left(\frac{-DBH_i}{\beta}\right)\right) \times \varepsilon_i, \quad \varepsilon_i \sim LN(0, \sigma^2) \quad \text{Eqn. 3}$$

M4 (Michaelis-Menten, eqn. 4): This non-linear model, while very common in chemistry, has rarely been employed to model height-DBH relationships (Huang, Titus & Wiens 1992). However, it presents all the required features: positive, increasing, with an oblique tangent line with slope $\beta = \alpha/\gamma$ in (0, 0) and a horizontal asymptote $H = \alpha$ when DBH is large.

$$H_i = \frac{\alpha \times DBH_i}{\gamma + DBH_i} \times \varepsilon_i, \quad \varepsilon_i \sim LN(0, \sigma^2) \quad \text{Eqn. 4}$$

The model was re-arranged as follow to ease the parameter inference:

$$H_i = \frac{1}{1/\alpha + \beta/DBH_i} \times \varepsilon_i, \quad \varepsilon_i \sim LN(0, \sigma^2) \quad \text{Eqn. 5}$$

All models have 3 parameters: 2 for the shape and 1 for the variance of the error term. In order to mechanistically increase the model uncertainty with height and DBH, the error term was modeled by a Log-Normal distribution. Keeping in mind our objective is biomass prediction, each height-DBH observation was weighted by a proxy w_i of the biomass of each single tree (Eqn. 6)

$$w_i = DBH_i^2 \times H_i \quad \text{Eqn. 6}$$

The weights w_i were normalized in each plot to sum to the number of observations.

The models M1 to M4 were calibrated in each forest plot. Parameter estimations were conducted using MCMC methods (see Supplementary Material S1). After discarding a burn-in sample and a thinning of the chains, 1 000 samples of the posterior distribution of each parameter is kept (for M4, the posterior distribution of the parameters are presented on fig. 1). The models inferred independently in each forest plot are referred to as the “site-specific” height-DBH model.

Height-DBH model shape selection

For each forest plot, the AGB of the plot was computed. The AGB of a forest plot is the sum of the AGB of the trees from this plot divided by the surface of the plot, in $\text{Mg} \cdot \text{ha}^{-1}$. The tree AGB model predicts the mass of a tree from its DBH, height, and WSG (eqn. 7). Uncertainties from height predictions, WSG predictions, and tree AGB model parameters are propagated through Monte-Carlo samples of their respective distributions (Molto, Rossi & Blanc in press).

$$\log(AGB_i) = \beta_0 + \beta_1 \log(DBH_i) + \beta_2 \log(H_i) + \beta_3 \log(WSG_i) + \varepsilon_i, \quad \varepsilon_i \sim \mathcal{N}(0, \sigma^2) \quad \text{Eqn. 7}$$

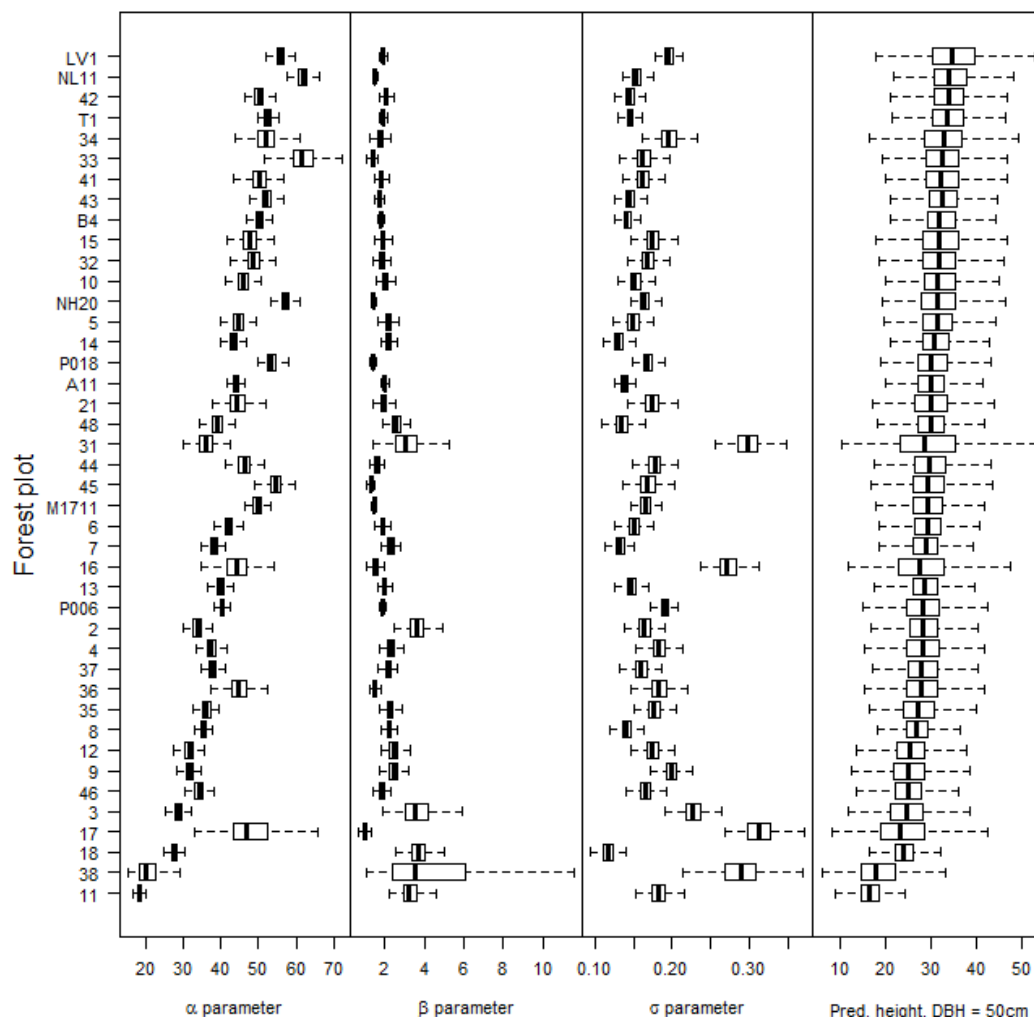


Figure1: Posterior distribution of the α , β , and σ coefficients of the M4 model: $H_i = \frac{1}{\frac{1}{\alpha} + \frac{\beta}{DBH_i}} \times \varepsilon_i$, $\varepsilon_i \sim LN(0, \sigma^2)$. The last panel presents the predicted height distribution of a tree with a DBH of 50 cm.

In each forest plot, AGB was predicted 1- using field-measured heights, 2- with predicted heights. When the AGB of a tree was predicted (eqn. 7) with a height H_i predicted from one of the four height models, Monte-Carlo samples of the predicted height H_i are generated from the posterior samples of the parameters and error term of the height-DBH model.

The forest plot's AGB distributions obtained from each height predictions were compared with the AGB distribution obtained from measured height using the RMSE (Root mean squared error) (fig. 2). The selected height-DBH model was thereafter noted M^* .

In addition, the selected model M^* was calibrated on the entire dataset without site effect. This model is called “regional” model.

Environment and forest structure effect on the height model parameters

Model definition

A new model was built where the shape parameters α and β in the selected model M^* was replaced by a log-linear combination of the variables x_j describing the forest plots p (Eqn 7). The parameter σ was now unique and we did not try to explain its plot-to-plot variation for identifiability reasons. The variables x_j were scaled so the coefficients of the log-linear combination can be compared to each other.

We used the exponential function to constrain the values of the parameters α_p and β_p to be positive. In the models M2, M3, and M4, the coefficients α and β are positive for physical reasons: the height is a positive value and the height increases with the DBH. In the model M1, the α parameter is not necessarily positive. The observations were weighted as previously (eqn. 6). For algorithm details of the estimation of θ_α , I_α , θ_β , and I_β , see Supplementary Material S1.

$$\alpha_p = \exp\left(\theta_{\alpha_0} + \sum_j \theta_{\alpha_j} i_{\alpha_j} x_{j,p}\right), \quad \beta_p = \exp\left(\theta_{\beta_0} + \sum_j \theta_{\beta_j} i_{\beta_j} x_{j,s}\right) \quad \text{Eqn. 7}$$

We used the method set by Kuo and Mallick (1998) to select the variables x_j to be integrated in the final model. During parameter inference (see Supplementary material S1), an indicator i_{α_j} (respectively i_{β_j}) associated with each variable x_j for the parameters α (respectively β) can take two values: 1 indicates that the variable is kept in the model, 0 indicates that the variable is not kept in the

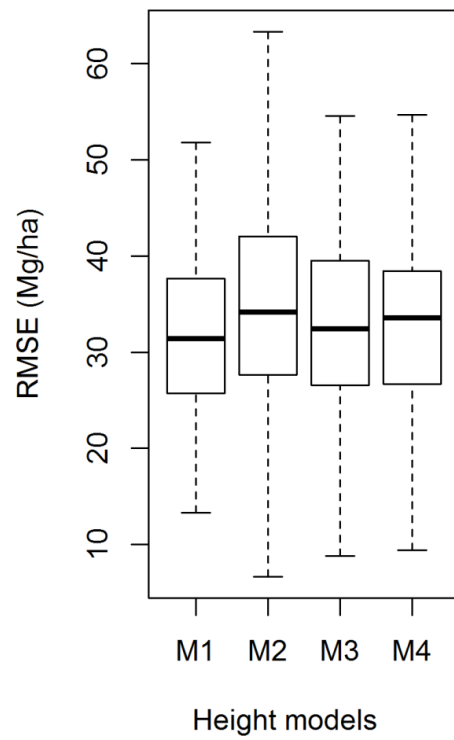


Figure 2: Boxplots of the mean RMSE of the AGB predictions in the 42 forest plots with tree heights predicted by four different models: log-linear (M1), log-log (M2), Weibull (M3), and Michaelis-Menten (M4).

model (eqn. 7). Thanks to the indicators, the MCMC algorithm explores different combinations of variables.

To decide whether a variable x_j is kept in the model or not, we compute its percentage of presence in the explored models. This percentage is computed as the mean of the MCMC chain values of the indicator $i_{\alpha j}$ after a burn-in removal and a thinning.

Usually, this percentage had the shape of a plateau followed by a rapid decrease. We aimed to keep the variables with a percent of selection close to the value of the plateau. The selected variables implicated in the replacement of α and β are not necessarily the same (figure 3).

Variable selection

Because the environment has an obvious effect on the forest structure, we could not consider the structure and environmental variables in a single step. Thus, we first replaced the α and β coefficients by a linear combination of the stand structure variables only. The structure variables were selected with the method described above. The resulting model is called “stand structure model” (figure 3, panels 1 and 3).

Then, the environment variables were added to the previous stand structure model. The variable selection procedure was run again, selecting the environment variables only. In other words, an environmental variable was selected only if it caught residual variance that was not caught by the formerly-selected structure variables (figure 3, panels 2 and 4).

As for the comparison of the model shapes, the heights predicted with the stand structure model and the environment model were used to compute the AGB of the plots. In its ability to predict height to predict AGB, the best model including structure and eventually environmental variables are a compromise between the regional model (worst case) and the site-specific model (best case). The comparison of the AGB prediction RMSE allows quantifying how the variables describing the forest plots improve the regional model and how far the performances are from the site-specific model.

Variable j	θ_{α_j} Median and 95% CI	θ_{β_j} Median and 95% CI
Intercept	3.785 [3.755, 3.802]	0.595 [0.553, 0.634]
Basal area	-0.017 [-0.027, -0.008]	
Prop_10-20	-0.135 [-0.146, -0.12]	0.11 [0.098, 0.136]
Prop_40-60	-0.023 [-0.036, -0.004]	
Prop_60+		0.044 [0.032, 0.055]
slope	0.025 [0.015, 0.036]	
rainfall	-0.028 [-0.048, -0.008]	0.051 [0.023, 0.081]
log_area_drain		-0.04 [-0.048, -0.033]

Table 1: Median and 95% Confidence Interval (CI) of the effects of structure variables and environment variables on coefficients α and β of the model M4 (eqn. 5, eqn. 7, fig. 3).

RESULTS

Model shape selection

Overall, we found that α and β coefficients were different from one site to another (Figure 1 for M4 model), showing that the height-DBH relationship varies between locations. The posterior distributions of both parameters α and β were somewhat correlated ($r = -0.81$), suggesting that the forest properties they catch are not independent. Using the α , β , and σ coefficients of the site-specific M* model, the heights were predicted with each model in each forest plot for a tree of 50 cm DBH (figure 1).

RMSEs being quite similar and completely overlapping (Figure 2), we chose to focus on model M4 for two main reasons: 1- it has biological-meaningful coefficients (contrary to M1 and M2); 2- it is easier to manipulate than M3 and its exponential function.

Environment and structure variable selection

The selected structure variables explaining the observed variation of α are the basal area (negative effect), the proportion of small stems (strong negative effect), and the proportion of medium stems (negative effect). In addition, the slope (positive effect) and the rainfall (negative effect) were selected among the environment variables (figure 3, table 1).

The selected structure variables involved in the replacement of β are the proportion of small stems (strong positive effect) and the proportion of bigger stems (positive effect). The rainfall (positive effect) and the drained area (negative effect) were selected among the environment variables (figure 3, table 1) to complete the structure variables.

The variables selected for the replacement of α and β are not shared. All the found parameters exclude zero from their 95% confidence interval. The highest values were obtained for the proportion of small stems, highlighting its great explicative power. Environmental variables have very weak effects.

AGB prediction

The RMSE of the model including structure and/or environment variables was larger than the RMSE of the site-specific model and smaller than the RMSE of the universal model (figure 4). The RMSE of the model including environment variables did not differ from the RMSE of the model using structure variables only (figure 4).

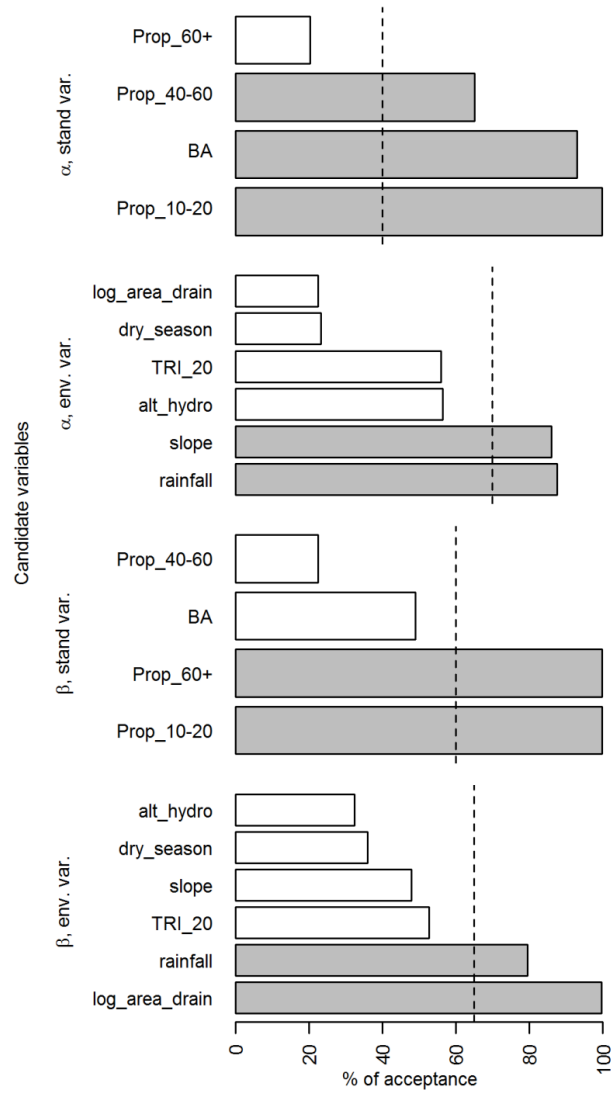


Figure 3: Variable selection. The bars represent the % of presence of the variables in the model, computed from the posterior values of the indicators i_{α_j} and i_{β_j} (eqn. 7). The dotted lines indicate, in each selection process, which cut-off limit is chosen for the acceptance of a variable in the definitive models. “Prop_X_Y” = proportion of stems between X and Y cm, “BA” = Basal Area, TRI_20 = Terrain Ruggedness Index.

The grey bar indicates the variables kept in the definitive model. The structure variables (first and third panels) were selected first. Then, keeping the selected structure variables, environmental variables were added to improve the model (second and last panels).

DISCUSSION

Using a dataset from diverse neotropical forests from French Guiana, we modeled the height-DBH relation using the Michaelis-Menten equation. The height-DBH relation was varying between locations, affecting the AGB estimations.

We then demonstrated that part of the height-DBH relation variability can be explained by variables issued from the forest structure and, less, from descriptors of the local environment.

Model choice and Parameter values in the site-specific model

On their performances to predict height to predict AGB, the 4 models were very close each other. We believed that our peculiar weighting was responsible for this tightness, because it gave a high weight to the trees with a high biomass. This suggested that, with these weights, one can use any of these four models to predict heights to predict biomass. However, the replacement of the parameters by combinations of environment variables may be different. We also emphasize that the Michaelis-Menten model mathematical form is the easiest to handle (no exponential function). Though the exponential model has been used in the past, Feldpausch *et al.* (2012) found that the Weibull model was the most appropriate for biomass prediction (they did not consider the Michaelis-Menten model). We thus conclude that asymptotic models should be preferred to other shapes.

The α and β model parameters differed largely between forest plots (figure 1). This demonstrates that the height-DBH relationship was not the same in each plot, leading to contrasting height-DBH relationships and contrasting AGB values.

The α parameters represented the value of the horizontal asymptote for the largest DBH. This value was highly correlated with the maximum observed height in each forest plot ($\alpha = 1.06 * H_{max}$, $R^2 = 0.98$, $RSE = 6.7$). This result has important practical consequences. If it is not reasonable to measure the height of all trees in large-scale inventories, but it is feasible to measure the 10 higher trees or so to get the maximum height of a forest plot. Moreover, the maximum height of a forest plot is a direct output from LiDAR measurements. In either of these cases, the α parameter won't be predicted from environmental variables but will be estimated more or less directly. Knowing the α parameter, the construction of the Height-DBH model is more simple, straightforward, and precise because it depends only on finding β .

The β parameter represented the slope of the oblique tangent in (0, 0). The larger β is, the faster the trees reach the asymptote. β values showed less variation than α between forest plots (figure 1). This suggests that the parameter could be inferred at the region level, with no site effect on its value. However, because some plot to plot differences remained, we decided to test the forest structure and environment effect on this parameter. If one aims to build a height-DBH model estimating α as suggested above, one could consider using a constant β parameter for simplicity.

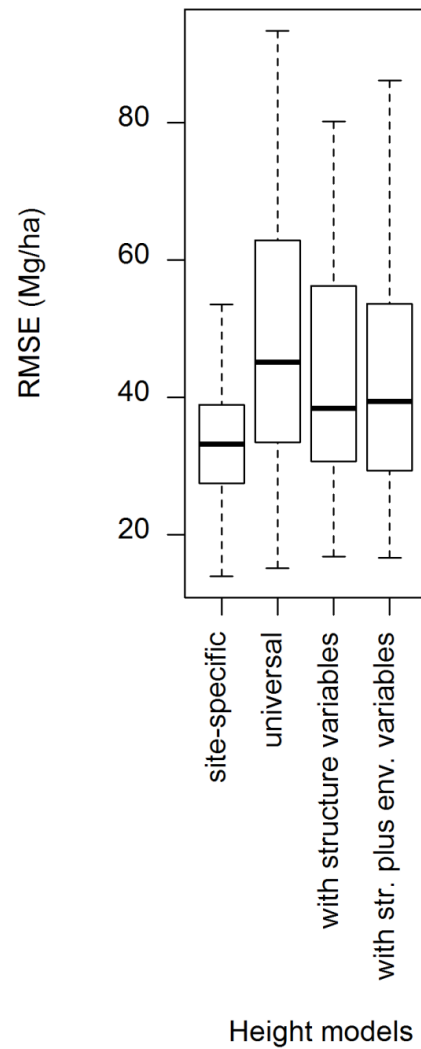


Figure 4: Boxplots of the mean RMSE of the AGB predictions in the 42 forest plots with tree heights predicted by four different height-DBH models: site-specific, universal, based on structure variables, and based on structure variables completed with environment variables.

Structure variables

The competition for light between trees has been identified as a major driver of the tree's height trajectory. Some authors suggest that the Basal area is a better expression of the competition than the stem density (Hummel 2000; King *et al.* 2009). However, we found a weak and negative effect of BA on α and it was not kept for β explanation.

In our case-study, we believe that the height-DBH relationship variation is better explained by the forest succession. After perturbation, plants compete for resources. The younger stands contain a high proportion of small trees, while self-thinning rules cause the older stands to contain a relatively small number of large trees (Clark 1996; Guariguata & Ostertag 2001; Luyssaert *et al.* 2008). Indeed, the proportion of small trees (10-20 cm DBH) has a strong positive effect on β together with a strong negative effect on α . In a young forest patch with high density of small trees, the tree competition cause trees to grow faster in height (Hummel 2000), but the relative youth of the forest patch may also cause the forest stand to have lower maximum heights (effect on α). The small positive effect of the proportion of biggest trees (more than 60cm DBH) on β also suggests that the presence of a large tree, limiting the light resource, also cause the small trees to grow faster in height.

Environment variables

Because the environment has an obvious effect on the forest structure (Baraloto *et al.* 2011), we decoupled in time the inclusion of structure and environment variables in the final model. The negative effect of the rainfall on α is clearly unexpected. The rainfall, related to the water availability, has largely been described as a positive driver of the forest height (Koch *et al.* 2004; Ryan, Phillips & Bond 2006).

The negative effect of the drained area on β indicates that the trees grow slower in height in a seasonally flooded or waterlogged terrain. This is explained by (i) a greater light availability (Ferry *et al.* 2010) in turn linked to higher turnover rates (Madelaine *et al.* 2007; Ferry *et al.* 2010) and (ii) higher mechanical constraints due to the lower soil stability in flooded areas (Gale & Barfod 1999; Gale & Hall 2001).

The trade-offs between variables in α and β replacements, between α and β replacements, and the low values of the model parameters makes that we should consider the highlighted patterns carefully.

Perspectives

In this study we showed that part of the variability of the height-DBH relationship was mainly explained by the maturity of the stand, expressed as the proportion of small trees (10-20 cm DBH). While Basal Area and rainfall were the most important variables at world scale (Feldpausch *et al.* 2011), we did not find them crucial at the regional scale in French Guiana. Our study did not include any soil effect on the Height-DBH relationship, though we interpreted the effect of high drained areas

as a possible indicator of soil instability. If available, information on the soil properties has been proved to be meaningful when studying the tree's heights (Aiba & Kitayama 1999; Quesada *et al.* 2009; Feldpausch *et al.* 2011).

To go even further, more sophisticated model could be inferred incorporating much more information at the tree level. For example, if the botanical information is available, a trait-based model may provide substantial improvement. The functional traits have proven to catch information on species biological properties that may be related to the Height-DBH relationship (Baraloto *et al.* 2010b; Hérault *et al.* 2011).

Now the model can be used to predict the coefficients of a height-DBH model on the whole region of French Guiana. The new AGB estimates using the new predicted height will help us to understand the spatial patterns of AGB variations and produce more accurate Carbon stock estimates.

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REFERENCES

- Aiba, S.-i. & Kitayama, K. (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology*, **140**, 139-157.
- Araujo, T.M., Higuchi, N. & Junior, J.A.D. (1999) Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Para, Brazil. *Forest Ecology and Management*, **117**, 43-52.
- Asner, G.P., Powell, G.V.N., Mascaro, J., Knapp, D.E., Clark, J.K., Jacobson, J., Kennedy-Bowdoin, T., Balaji, A., Paez-Acosta, G., Victoria, E., Secada, L., Valqui, M. & Hughes, R.F. (2010) High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 16738-16742.
- Baccini, A., Goetz, S.J., Walker, W.S., Laporte, N.T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P.S.A., Dubayah, R., Friedl, M.A., Samanta, S. & Houghton, R.A. (2012) Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change*, **2**, 182-185.
- Baraloto, C., Paine, C.E.T., Patino, S., Bonal, D., Herault, B. & Chave, J. (2010a) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, **24**, 208-216.
- Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., Davila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V.A. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677-2688.
- Baraloto, C., Timothy Paine, C.E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patiño, S., Roggy, J.-C. & Chave, J. (2010b) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*, **13**, 1338-1347.
- Bock, M., Boehner, J., Conrad, O., Koethe, R. & Ringeler, A. (2004) SAGA GIS. pp. System for Automated Geoscientific Analyses.
- Brown, S. (1997) Estimating biomass and biomass change of tropical forests: A Primer. *FAO Forestry Paper 134*, pp. 55. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
- Brown, S., Gillepsie, A.J.R. & Lugo, A.E. (1989) Biomass estimation methods for tropical forests with applications to forestry inventory data. *Forest Science*, **35**, 881-902.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87-99.
- Clark, D.B. (1996) Abolishing virginity. *Journal of Tropical Ecology*, **12**, 735-739.
- Fang, Z.X. & Bailey, R.L. (1998) Height-diameter models for tropical forests on Hainan Island in southern China. *Forest Ecology and Management*, **110**, 315-327.
- Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djangbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., Franca, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patino, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrod, F., Sonke, B., Taedoumg, H.E., Tan, S., White, L., Woll, H. & Lloyd, J. (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences*, **8**, 1081-1106.
- Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brien, R.J.W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard, C., G.A., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J., Comiskey, J.A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djangbletey, G., Domingues, T.F., Erwin, T.L.,

- Fearnside, P.M., França, M.B., Freitas, M.A., Higuchi, N., C, E.H., Iida, Y., Jiménez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe, D.J., Mitchard, E.T.A., Neill, D.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., Peh, K.S.H., Pena Cruz, A., Peñuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G.M.F., Vásquez, R., Vilanova, E., Vos, V.A., White, L., Willcock, S., Woell, H. & Phillips, O.L. (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, **9**, 3381-3403.
- Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**, 106-116.
- Gale, N. & Barfod, A.S. (1999) Canopy tree mode of death in a western Ecuadorian rain forest. *Journal of Tropical Ecology*, **15**, 415-436.
- Gale, N. & Hall, P. (2001) Factors determining the modes of tree death in three Bornean rain forests. *Journal of Vegetation Science*, **12**, 337-348.
- Gibbs, H.K., Brown, S., Niles, J.O. & Foley, J.A. (2007) Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters*, **2**, -.
- Gond, V., Freycon, V., Molino, J.-F., Brunaux, O., Ingrassia, F., Joubert, P., Pekel, J.-F., Prévost, M.-F., Thierron, V., Trombe, P.-J. & Sabatier, D. (2011) Broad-scale spatial pattern of forest landscape types in the Guiana Shield. *International Journal of Applied Earth Observation and Geoinformation*, **13**, 357-367.
- Guariguata, M.R. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, **148**, 185-206.
- Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C.E.T., Wagner, F. & Baraloto, C. (2011) Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology*, **99**, 1431-1440.
- Houghton, R.A., Lawrence, K.T., Hackler, J.L. & Brown, S. (2001) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology*, **7**, 731-746.
- Huang, S.M., Titus, S.J. & Wiens, D.P. (1992) Comparison of Nonlinear Height Diameter Functions for Major Alberta Tree Species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **22**, 1297-1304.
- Hummel, S. (2000) Height, diameter and crown dimensions of *Cordia alliodora* associated with tree density. *Forest Ecology and Management*, **127**, 31-40.
- IPCC (2000) IPCC Good Practice Guidance and Uncertainty Management in National Greenhouse Gas Inventories. Hayama, Kanagawa, Japan.
- King, D.A., Davies, S.J., Tan, S. & Nur Supardi, M.N. (2009) Trees approach gravitational limits to height in tall lowland forests of Malaysia. *Functional Ecology*, **23**, 284-291.
- Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. *Nature*, **428**, 851-854.
- Kuo, L. & Mallick, B. (1998) Variable Selection for Regression Models. *Sankhyā: The Indian Journal of Statistics*, **60**, 65-81.
- Lucas, R.M., Honzak, M., Amaral, I.D., Curran, P.J. & Foody, G.M. (2002) Forest regeneration on abandoned clearances in central Amazonia. *International Journal of Remote Sensing*, **23**, 965-988.
- Luyssaert, S., Schulze, E.D., Borner, A., Knohl, A., Hessenmoller, D., Law, B.E., Ciais, P. & Grace, J. (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213-215.
- Madelaine, C., eacute, lissier, R., Vincent, G., Molino, J.F., Sabatier, D., Pr, vost, M.F. & de Namur, C. (2007) Mortality and recruitment in a lowland tropical rain forest of French Guiana: effects of soil type and species guild. *Journal of Tropical Ecology*, **23**, 277-287.
- Molto, Q., Rossi, V. & Blanc, L. (in press) Error propagation for biomass estimation in tropical forests. *Methods in Ecology and Evolution*.

- Nogueira, E.M., Nelson, B.W., Fearnside, P.M., Franca, M.B. & Alves de Oliveira, A.C. (2008) Tree height in Brazil's 'arc of deforestation': Shorter trees in south and southwest Amazonia imply lower biomass. *Forest Ecology and Management*, **255**, 2963-2972.
- Quesada, C.A., Lloyd, J., Anderson, L.O., Fyllas, N.M., Schwarz, M. & Czimczik, C.I. (2009) Soils of amazonia with particular reference to the rainfor sites. *Biogeosciences Discuss.*, **6**, 3851-3921.
- Ryan, M.G., Phillips, N. & Bond, B.J. (2006) The hydraulic limitation hypothesis revisited. *Plant Cell and Environment*, **29**, 367-381.
- Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M. & Morel, A. (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 9899-9904.
- Sharma, M. & Parton, J. (2007) Height–diameter equations for boreal tree species in Ontario using a mixed-effects modeling approach. *Forest Ecology and Management*, **249**, 187-198.
- USGS (2004) Shuttle Radar Topography Mission. (ed. U.o.M. Global Land Cover Facility). College Park, Maryland.
- Wagner, F., Herault, B., Stahl, C., Bonal, D. & Rossi, V. (2011) Modeling water availability for trees in tropical forests. *Agricultural and Forest Meteorology*, **151**, 1202-1213.
- Wagner, F., Rossi, V., Stahl, C., Bonal, D. & Herault, B. (2012) Water availability is the main climate driver of neotropical tree growth. *PloS one*, **7**, e34074.

SUPPLEMENTARY MATERIAL

Supplementary Material S1: Variable selection algorithm

We consider the following model for the height H_i of a tree i in the forest plot p , for $i=1, \dots, n$. The plots are described by d variables x_1, \dots, x_d . The indicators i_{α_j} and i_{β_j} indicates the presence (1) or absence (0) of the j -th variable in the model. The parameters to be inferred are θ_{α_j} , i_{α_j} , θ_{β_j} , i_{β_j} , and σ for $j=1, \dots, d$.

$$H_i = \frac{1}{1/\alpha_p + \beta_p/DBH_i} \times \varepsilon_i, \quad \varepsilon_i \sim LN(0, \sigma^2)$$

$$\alpha_p = \exp\left(\theta_{\alpha_0} + \sum_j \theta_{\alpha_j} i_{\alpha_j} x_{j,p}\right), \quad \beta_p = \exp\left(\theta_{\beta_0} + \sum_j \theta_{\beta_j} i_{\beta_j} x_{j,p}\right)$$

where LN is the log-normal distribution.

Estimations of α_p and β_p are available from the site-specific model. A rough maximum likelihood estimates (MLE) of θ_{α_j} and θ_{β_j} can be obtained with a linear model linking the site specific α_p and β_p to the variables x_j .

We did weighted regression because we wanted our model being more accurate for large trees. For the tree i , we used the weight w_i as a proxy of the tree biomass:

$$w_i = DBH_i^2 \times H_i$$

$Hobs_i$ and $Hpred_i$ are respectively the observed height and the predicted height for the tree i :

$$Hpred_i = \frac{1}{1/\alpha_p + \beta_p/DBH_i}$$

The likelihood function is given by:

$$\mathcal{L}(\theta_{\alpha}, i_{\alpha}, \theta_{\beta}, i_{\beta}, \sigma^2 | DBH, H) = \prod_{i=1}^n dlnorm(Hobs_i, Hpred_i, \sigma^2) w_i$$

Where $dlnorm$ is the density function of the lognormal distribution. The model inference was done though the Bayesian paradigm; parameters were attributed standard low-informative priors.

For our model a Kuo-Mallick algorithm is defined by:

Repeat:

For each variable x_j in a random order:

Compute the MLE of $\theta_{\alpha_{MVE}}$ in the current model including the variable j .

Generate $\theta_{\alpha_j}^*$ from a normal proposition distribution centered on $\theta_{\alpha_{MVE}}$ with variance 0.1

Reject or accept the proposition with the Metropolis ratio

Compute the likelihood ratio:

$$r = \frac{\mathcal{L}(\theta_\alpha, i_\alpha(i_{\alpha_j} = 1), \theta_\beta, i_\beta, \sigma^2 | DBH, H)}{\mathcal{L}(\theta_\alpha, i_\alpha(i_{\alpha_j} = 0), \theta_\beta, i_\beta, \sigma^2 | DBH, H)}$$

Generate i_{α_j} from a Bernoulli distribution $\mathcal{B}(p = \frac{1}{1+r})$

(Note: the intercepts θ_{α_0} and θ_{β_0} are always included in the model).

With the same process, update θ_β and i_β .

Compute

$$V = \sum_i w_i \left(\log(H_{obs_i}) - \log(H_{pred_i}) \right)^2$$

Generate σ^2 from an inverse-gamma distribution $\text{InvG}(\text{prior} + \frac{nind}{2}, \text{prior} + \frac{V}{2})$.

We discard the beginning of the chains (burn-in) and use a thinning to reduce autocorrelation.

Supplementary Material 2: Forest plots description

Plot ID	log_area_ drain	slope (rad)	TRL_20	alt_hydro (m)	rainfall (mm)	dry season index (month)	BA (m ² /ha)	prop_stem _1 (%)	prop_stem _2 (%)	prop_stem _3 (%)	prop_stem _4 (%)	α	β	Fresh AGB (t/ha)
38	9.00	0.24	205.48	245.53	3040.05	2.53	10.05	88.71	10.75	0.54	0.00	19.21	2.43	71.29
11	9.00	0.18	104.44	115.12	3167.78	2.73	29.77	91.50	7.52	0.65	0.33	18.27	3.00	202.86
48	9.00	0.05	236.65	285.70	2661.64	2.45	19.20	70.05	25.60	3.38	0.97	38.78	2.55	225.50
2	9.00	0.01	6.89	11.95	2370.99	3.32	28.30	77.97	20.05	1.49	0.50	33.70	3.55	301.47
36	11.40	0.16	106.10	0.00	3039.15	2.53	28.85	71.43	23.21	4.29	1.07	44.45	1.50	328.77
46	10.10	0.14	21.05	0.00	2665.66	2.44	37.21	77.22	16.71	5.57	0.51	33.77	1.77	386.27
3	10.61	0.01	7.59	7.75	2383.91	3.30	38.52	78.81	15.25	4.13	1.81	29.11	3.24	413.68
35	9.00	0.07	62.30	47.97	3038.09	2.53	37.18	86.54	8.76	3.21	1.50	35.91	2.31	426.39
18	9.00	0.50	88.42	112.86	3167.48	2.73	48.09	79.88	18.34	1.48	0.30	27.61	3.52	459.64
A11	9.00	0.14	15.72	22.78	2302.08	3.36	34.47	55.68	29.55	10.91	3.86	44.14	1.98	464.88
B4	9.00	0.06	18.82	22.87	2378.35	2.99	34.14	56.58	29.61	12.06	1.75	50.02	1.79	465.22
37	15.34	0.01	87.80	0.00	3031.37	2.52	39.59	84.71	10.35	3.76	1.18	37.56	2.16	481.16
16	13.59	0.01	44.92	0.13	3168.00	2.72	44.74	72.79	21.48	3.58	2.15	42.36	1.57	485.12
21	9.00	0.03	21.27	28.50	2400.63	3.25	39.19	59.47	29.07	9.25	2.20	43.34	1.90	496.64
4	9.00	0.01	16.87	21.73	2376.31	3.33	40.49	68.91	22.12	7.69	1.28	37.14	2.29	498.31
17	9.69	0.11	23.53	6.64	3167.87	2.72	49.56	58.99	30.90	7.30	2.81	41.43	1.10	503.94
15	9.00	0.06	28.37	37.65	3167.19	2.70	44.64	82.86	13.37	2.45	1.32	46.54	1.85	521.55
P018	10.39	0.12	8.47	3.22	2545.89	3.70	38.16	58.10	28.29	9.07	4.54	53.44	1.43	533.19
9	9.00	0.11	8.95	11.27	2403.37	3.25	47.90	65.43	27.16	5.68	1.73	31.94	2.32	537.01
M1711	9.00	0.10	72.27	86.47	3137.00	2.62	39.97	60.61	26.26	8.28	4.85	49.53	1.47	540.11
5	9.00	0.02	12.64	18.44	2370.64	3.33	40.17	60.61	27.65	7.58	4.17	44.10	2.18	562.40
41	9.00	0.09	31.20	38.10	2665.35	2.44	43.32	64.02	27.13	5.49	3.35	49.76	1.85	568.14
10	10.10	0.06	41.11	4.02	3167.97	2.73	40.79	63.60	26.15	7.07	3.18	45.55	2.05	568.49
P006	11.08	0.05	10.04	3.26	2558.00	3.66	46.23	57.23	31.80	8.74	2.23	40.53	1.89	588.20
31	9.00	0.06	95.62	19.67	3032.44	2.52	45.28	63.57	26.12	5.84	4.47	38.63	2.43	593.74
NL11	10.39	0.29	64.65	27.60	3026.66	2.51	39.05	61.87	26.77	5.88	5.48	61.26	1.50	594.04
33	10.10	0.15	87.10	22.37	3037.09	2.53	40.34	62.24	25.73	5.39	6.64	60.39	1.41	601.11
12	9.00	0.11	63.77	76.47	3167.96	2.72	62.92	75.07	21.98	2.41	0.54	31.67	2.39	610.27
7	11.08	0.04	10.42	0.50	2390.11	3.29	52.05	65.95	24.70	6.95	2.40	37.90	2.34	626.77
LV1	9.69	0.10	20.68	18.42	3131.50	2.77	43.93	56.70	30.93	9.97	2.41	56.67	1.88	640.62
NH20	9.00	0.02	92.19	24.25	3032.96	2.52	45.10	54.62	30.52	9.64	5.22	56.82	1.45	673.33
T1	9.00	0.14	24.13	28.80	3093.72	2.86	43.66	50.49	32.28	10.44	6.80	52.33	1.94	706.67
34	9.00	0.20	68.92	79.82	3036.05	2.52	47.05	61.11	24.81	7.41	6.67	50.92	1.77	707.59
32	9.69	0.16	84.49	34.60	3033.48	2.52	48.85	55.56	28.97	9.52	5.95	48.90	1.74	720.90

Plot ID	log_area_drain	slope (rad)	TRL_20	alt_hydro (m)	rainfall (mm)	dry season index (month)	BA (m ² /ha)	prop_stem_1 (%)	prop_stem_2 (%)	prop_stem_3 (%)	prop_stem_4 (%)	α	β	Fresh AGB (t/ha)
6	9.00	0.11	19.24	25.65	2393.45	3.28	49.76	56.02	30.29	7.47	6.22	41.83	1.85	732.48
42	9.00	0.05	83.95	19.54	2662.55	2.45	52.48	60.85	30.16	6.35	2.65	49.82	2.10	744.26
14	9.00	0.08	36.23	40.92	3167.50	2.72	52.09	59.32	27.46	7.46	5.76	43.33	2.18	756.10
8	10.39	0.04	12.37	0.00	2391.19	3.27	62.19	60.64	28.71	8.42	2.23	35.01	2.23	768.01
13	9.00	0.17	75.73	91.94	3167.65	2.73	65.86	63.85	27.06	5.84	3.25	39.73	2.01	808.75
45	15.96	0.03	54.92	0.00	2663.14	2.44	55.21	50.94	32.45	12.08	4.53	53.88	1.35	817.43
44	9.00	0.02	15.21	3.89	2664.67	2.44	58.30	63.25	24.10	7.23	5.42	46.05	1.58	833.63
43	9.00	0.18	72.41	42.34	2666.06	2.45	59.77	64.37	25.75	7.36	2.53	51.28	1.79	841.05

Plot ID: Identification of the forest plots. ID starting with letters are the 1-ha plots; ID with numbers only are the 0.5-ha Gentry plots

log_area_drain: Logarithm of the drained area

TRL_20: Terrain Rugedness Index

alt_hydro: altitude above the closest stream of the hydraulic basin

BA: Basal Area

prop_stem_1: proportion of stems between 10cm and 20 cm DBH

prop_stem_2: proportion of stems between 20cm and 40 cm DBH

prop_stem_3: proportion of stems between 40cm and 60 cm DBH

prop_stem_4: proportion of stems above 60cm DBH

α : mean value of the alpha parameter

β : mean value of the beta parameter

Chapitre 5

Construction d'une carte de biomasse de la guyane française

Dans les chapitres 2, 3, et 4, nous avons mis en place des méthodes permettant l'estimation de la biomasse de parcelles inventoriées. Dans ce chapitre, nous étudions les variations spatiales de la biomasse pour essayer de prédire la biomasse en dehors des zones inventoriées.

Les parcelles inventoriées sont réparties dans la partie nord de la Guyane française. Notre jeu de données rassemble les inventaires de 4 projets : Inventaire papetier, Guyafor, Bridge, et Amalin. Les parcelles du projet Amalin sont réalisées conformément au protocole décrit dans le chapitre 2.

Dans chaque parcelle où les hauteurs ne sont pas mesurées, les hauteurs des arbres sont prédites par le modèle décrit dans le chapitre 4. Ensuite, la biomasse de chaque parcelle est prédite par le protocole décrit dans le chapitre 3, permettant la propagation des incertitudes.

Enfin, un modèle intégrant une composante d'autocorrélation spatiale relie

la biomasse des parcelles aux variables environnementales. L'incertitude associée aux estimations de biomasses des inventaires est propagée dans le modèle spatial par un processus de Monte-Carlo.

Nous démontrons que plusieurs variables environnementales ont un effet sur la biomasse. La topographie est une variable importante : les parcelles ayant une grande aire drainée ont des biomasses plus faibles. Comme attendu, nous observons un effet positif de la pluviométrie annuelle et un effet négatif de la durée saison sèche. Les différents substrats géologiques ont aussi des effets significatifs.

Finalement, nous sommes en mesure de produire une carte de biomasse pour la Guyane française. L'incertitude associée par toutes nos propagations conservatives est très importante (moyenne : 500 t/ha, écart-type : 200 t/ha). Cela vient d'une part du fait que l'incertitude de la biomasse des parcelles inventoriées est importante et d'autre part de la grande variabilité spatiale de la biomasse à petite échelle.

MAPPING BIOMASS OF TROPICAL FORESTS: UNCERTAINTY PROPAGATION WITH A MODEL-BASED APPROACH

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ABSTRACT

The recent increases of carbon emissions from human activities lead to an urgent need of the earth carbon stocks management. The tropical forests contain 40% of the world Carbon stocked in the vegetation. The countries owning tropical forests are encouraged to protect them from land-use change through the REDD+ and the Carbon market. To be efficient, these mechanisms require a precise mapping of Carbon stocks.

In this study, we estimated the biomass of a tropical region: French Guiana. Using appropriate and locally set models, we propagated the uncertainty from the fresh biomass estimation of individual trees to the biomass of the reference forest plot and the fresh biomass region map. The map was produced with a spatial variogram-based point-level model using environmental descriptors as covariates.

We found the topography to be an important factor at the 90m scale, with plots located on potentially waterlogged lands containing lower biomass. Rainfall, length of the dry season, geology, and vegetation types had also a significant effect on biomass.

Our results highlight the fact that AGB is highly contrasted at both local and regional scale. Our conservative uncertainty propagation leads to huge uncertainties: standard deviation is about 80% of the mean. The uncertainty of the estimation of the biomass of the forest plots and the very low spatial autocorrelation of the biomass are equally responsible for this uncertainty.

INTRODUCTION

The tropical forests store a large part of the earth carbon, with 40% of the earth's total terrestrial vegetation carbon (from 158 to 324 Pg (Gibbs *et al.* 2007)). Tropical countries are encouraged to reduce their carbon emissions from deforestation and land-use change (Pan *et al.* 2011) throughout the REDD+ program (IPCC 2000). Carbon maps associated with uncertainties of carbon stock estimates are an urgent need for a clear view of the potential effects of different management policies.

In the last decades, rough land-use maps have been easily built from aerial methods (Achard *et al.* 2002; DeFries *et al.* 2002). However, these methods failed to provide accurate estimates of AGB (Above-Ground Biomass) within areas covered with tropical forests (Sader *et al.* 1989; Mitchard *et al.* 2011). New tools are currently developed such as LIDAR (Asner *et al.* 2010; Vincent *et al.* 2012) or Radar (Daniel *et al.* 2010; Dubois-Fernandez *et al.* 2010; Ploton *et al.* 2011; Baccini *et al.* 2012). It is probably just a matter of years or decades before an adequate satellite signal treatment provides routinely worldwide and accurate biomass estimates for tropical forests.

Ground-based inventory data are another source of data to produce AGB mapping. In many countries forest national inventories are already available and could represent an alternative to remote-sensing approach for carbon stocks estimation (Gibbs *et al.* 2007). Moreover spatial variation in carbon stocks can be directly related with environmental gradients.

Many authors have reported factors that may explain AGB spatial variations but show little agreement (Houghton *et al.* 2001; Gibbs *et al.* 2007). The relation between AGB and forest stand structure is quite straightforward because the variables used to calculate AGB and to describe the stand structure are the same. AGB has been found to have strong correlation with stem density and basal area (Chave *et al.* 2004; Rutishauser *et al.* 2010). Tree height is also a key predictor of the AGB (Chave *et al.* 2004; Feldpausch *et al.* 2012; Molto, Rossi & Blanc in press). Less agreement exists for the Wood Specific Gravity (WSG) (Baker *et al.* 2004; Stegen *et al.* 2009).

At the tree scale, it has been described as an important predictor (Chave *et al.* 2005) and as a variable with no clear effect (Molto, Rossi & Blanc in press). At the regional scale, Baker *et al.* (2004) found WSG to explain large variation in the Amazon basin but Stegen *et al.* (2009) found no consistent relation between AGB and WSG. Nevertheless, in a biomass mapping perspective, neither forest stand structure nor WSG are available at large scale. They cannot be used for AGB extrapolations in space. The challenge is thus now to understand how environmental factors may affect the AGB through their effects on forest structure/properties (Baraloto *et al.* 2011).

At large scale, many authors agree upon a positive effect of the amount of annual rainfall and a negative effect of the length of the dry season (Dry Season Index, DSI) (Chave *et al.* 2004; Malhi *et al.* 2006). The effect of topography is debated between no effect (Clark & Clark 2000) and a negative effect in waterlogged bottomlands (Ferry *et al.* 2010).

In the present study, we explored the potentiality of environmental factors for AGB mapping at a large scale (millions of hectares) from an outstanding ground-based inventory database in French Guiana. Considering that spatially-explicit studies of the AGB variation (Rutishauser *et al.* 2010; Wagner *et al.* 2010) suggests that a spatial correlation model could be appropriate (Sales *et al.* 2007), we analyzed the relation between the AGB of French Guyana and the geology, a categorization of the canopy texture, topographical factors, hydrographic factors and climate factors, with a variogram-based spatial point model. The model was also used for biomass prediction outside the inventoried area. In addition, we propagated carefully the uncertainties of AGB estimations in the spatial model. The uncertainties are huge in AGB estimations (Chave *et al.* 2005; Pan *et al.* 2011; Saatchi *et al.* 2011; Molto, Rossi & Blanc in press). A reliable uncertainty estimation of AGB is necessary to allow proper comparison of AGB changes in space and time, as already pointed out by IPCC (Solomon *et al.* 2007).

Specifically, the objectives of the study were:

- 1- To propagate all the uncertainty while estimating the biomass of the census plots.
- 2- To analyze the relation between AGB and the environmental factors given the propagated uncertainty.
- 3- To produce a regional AGB map associated with an uncertainty map.

To our knowledge our study is the first attempt to produce a biomass map from heterogeneous field inventories while propagating all the uncertainties generated during the prediction process. This is a step forward in the community efforts to compute the carbon stocks and CO₂ emissions worldwide.

MATERIAL AND METHODS

Biomass estimation and uncertainty propagation

AGB was estimated in a given forest plot by summing the AGB estimated for each tree of the plot. The single tree biomass was estimated with a given AGB tree model linking some key-properties of a tree (DBH, height, WSG) with its dry mass. Because WSGs are never measured at the individual tree level when forest plots are inventoried, they have to be predicted. The WSG of a tree was predicted from its taxonomic identification with a WSG model. Where individual tree heights were not measured during the inventory, tree heights had also to be predicted from the diameter with height-diameter model (Figure 1). The uncertainties of predicted WSG and heights have to be propagated to the tree biomass estimation (Chave *et al.* 2004).

To produce an AGB map, we considered the AGB as continuous response surface over the region. This AGB surface was sampled at the inventory plots. The AGB surface was adjusted to the sample locations using kriging techniques with covariables describing the regional environment. The uncertainty in the AGB of the plot inventories has to be propagated through the spatial extrapolation model to the AGB map (Figure 1).

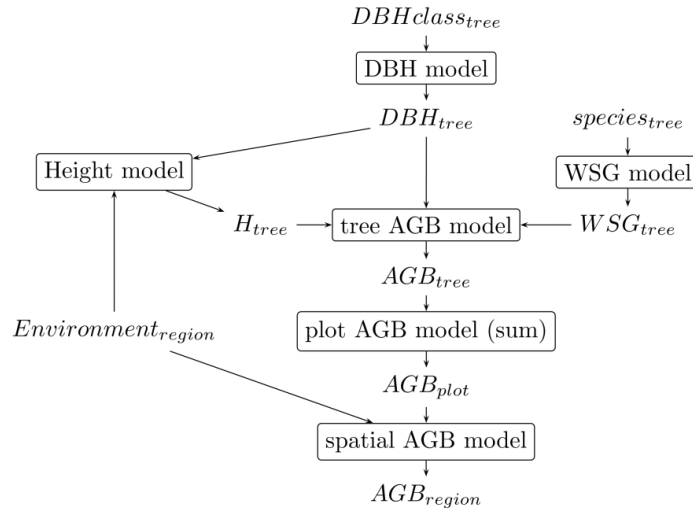


Figure 1: AGB map production steps. For each tree of each inventory forest plot, the WSG is predicted from the species identification of the tree and the tree height is predicted from the tree DBH if necessary. The sum of the tree's AGBs in each inventory plot gives the AGB of the inventory plots. The AGB of the inventories and the region environment descriptors are linked in a spatial model to produce an AGB map of the region.

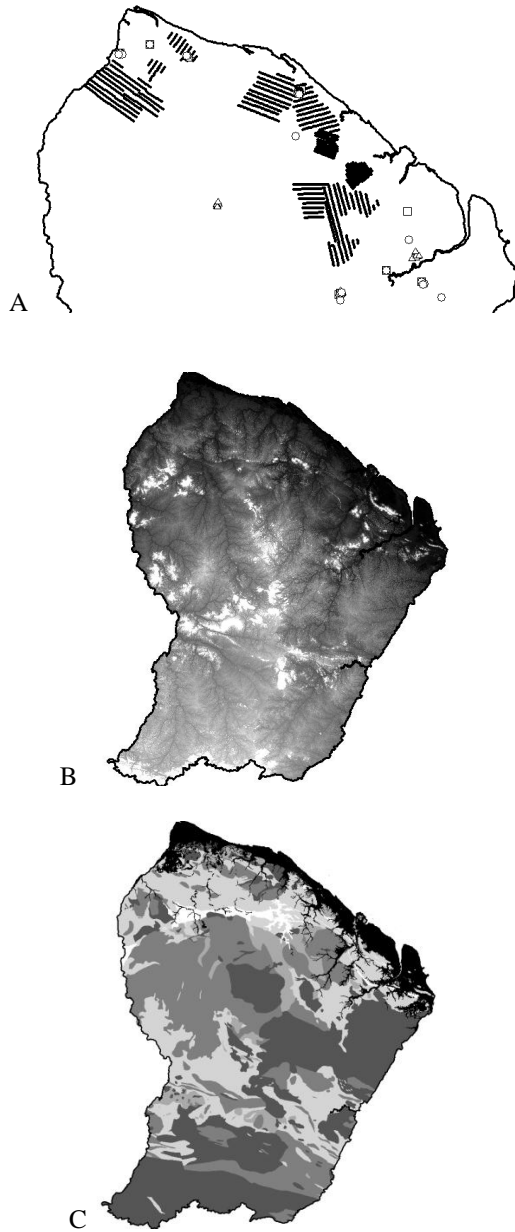


Figure 2: (A) Map of the census plots locations. Black points are “Inventaire Papetier” plots (1913 plots); triangles are the Guyafor plots (13 plots); circles are the Amalin plots (33 plots); squares are the Bridge plots (9 plots located within Guyafor plots). (B) SRTM altitude map. The altitude range is [0m (black), 850m (white)]. (C) Geology map (table 1).

French Guyana is located at 4°N 52°W , on the East coast of South America. The region is 401 km long on the N-S axis and 328 km wide on the E-W axis.

Data

Biomass data

The real biomass data consists in 361 trees logged and weighted in 1982 (Lescure *et al.* 1983). The trees were selected after a fast inventory to represent a range of diameter and heights. The DBH and the height of each tree were known but the WSG was not measured accordingly to our standard. WSG was predicted with the WSG model and its uncertainty propagated to the AGB tree model. At the difference of numerous authors, we worked on fresh biomass because it is what was really measured. The conversion to dry biomass and carbon content requires other models. These conversions were discussed in the discussion part.

WSG data

During the Bridge project, the WSG was measured for 2,504 trees in French Guiana, representing 466 species in 201 genera in 56 families (Baraloto *et al.* 2010; Sarmiento *et al.* 2011; Baraloto *et al.* 2012). Samples consisted of 6 mm long cores and thus contain sapwood only.

Height data

We used the height-diameter data collected during the Bridge project (9 one-hectare forest plots) and the Amalin project (42 half-hectare forest plots) (Baraloto *et al.* 2011) (Figure 2A). In each plot, the height of each tree was measured. Various methods were used and were regularly compared for consistency.

Inventories data

To adjust the AGB surface response, we aggregated three dataset: 33 half-hectares plots of the Amalin census (Baraloto *et al.* 2011), X plots (between 4 and 7 ha) of the GUYAFOR census including the 9 one-hectare intensively studied plots of the Bridge project (Rutishauser *et al.* 2010; Baraloto *et al.* 2012), and 1913 half-hectares plots of the “Inventaire Papetier” (Figure 2A).

Amalin is a network of recent plots located in contrasted landscapes of French Guyana (Baraloto *et al.* 2011). All trees were inventoried on a 0.1 ha area (DBH>10cm) or a 0.5 ha area (DBH>20cm). Tree heights were measured visually by trained experts.

GUYAFOR is a network of permanent plot located in French Guyana. In each plot, the trees are inventoried on a 2-year basis. We used the most recent census (2009-2011 depending on the plot). The floristic determination is now very high (up to 80%). For 9 of these plots, intensive data collection (tree height, botanical determination and WSG measurements) have been made with the Bridge project.

The “Inventaire Papetier” was conducted by the CTFT (Centre Technique Forestier Tropical became CIRAD in 1984) between 1972 and 1976. To assess the forest resources in French Guiana, the forest was divided in large blocks along the coast. Within the blocks, the forest was inventoried in 25*200m plots placed every 200-400m on parallel lines separated by 1-3km. The DBH was measured in 10cm classes, starting at 10cm, 15cm, or 20cm (Guitet *et al.* 2006).

Environment description data

We used 8 variables describing the French Guiana environmental gradients. The variables properties are summarized in the table 1. Two variables are categorical. First, the remotely sensed vegetation classes (RSLC) from the satellite Spot-4 data (Gond *et al.* 2011) indicates 5 forest classes (Table 1) at a 1 km² square resolution. Second, we used a geological map simplified from Delor *et al.* (2001) (Figure 2C, table 1).

Environnement variable	Short name	Description	Effect on AGB	Source	Scale
Geology	geol1	Recent sediments	-	(Delor <i>et al.</i> 2001)	Vector
	geol3	Granites	+		
	geol4	Gneiss	-		
	geol5	Gabbros	+		
	geol6	Volcanic sedimentary rock	0		
Vegetation (RSCL)	type_forest18	Low dense forest	0	(Gond <i>et al.</i> 2011)	1 km
	type_forest19	High forest with regular canopy	+		
	type_forest20	High forest with disrupted canopy	0		
	type_forest21	Mixed high and open forest	+		
	type_forest22	Open/palm forest	- (?)		
Topography	Slope	Slope	+	Nasa STRM (USGS 2004)	90 m
	TRI	Terrain Ruggedness Index	0		
Hydrography	Log_area_drain	Surface of the hydraulic basin	-		
	Alt_hydro	Altitude above the closest stream	0		
Climate	rainfall	Annual average rainfall	+	Nasa TRMM (2011)	8 km
	DSI	Dry Season Index	-		

Table 1: Description of the environment variables and their effects on AGB.

Four variables were computed from a Digital Terrain Model (DTM) with 90m-sided squared cells (NASA SRTM (USGS 2004)) (Figure 1B):

- 1- The drained area measures the surface of the hydraulic basin that flows through a cell. A low value indicates cells located at the border between two basins, whereas the highest values indicate cells located downstream.
- 2- The hydraulic altitude was computed from the 3rd order hydraulic system. The hydraulic altitude of a cell is its altitude above the closest stream of its hydraulic basin. Lowest values (including 0), indicate that the forest plot is potentially temporarily flooded while the highest values indicate that the forest plot is top-hill located.
- 3- The slope of each cell was computed with a 180 meters lag (2 cells).
- 4- The Terrain Ruggedness Index (TRI) was computed with a 20 cells lag (1800 meters) to catch the difference between flat and more mountainous landscapes.

Two environmental variables were computed from the NASA TRMM rainfall data on a resolution of 8 km. One was the annual average rainfall in the ten last years (in mm); the other was a dry season index (DSI), computed as the average number of months with a rainfall below the average evapotranspiration (Wagner *et al.* 2012). The dry season index quantifies the length of the annual hydraulic stress for trees.

All maps and geographical information were computed with SAGA (Bock *et al.* 2004). Models inference and data analysis were conducted with the R software (R-Core-Team 2012).

Models

Tree AGB model

The conventional variables for the prediction of the mass of a tree *AGB* are the DBH, the height *H*, and the WSG (Chave *et al.* 2005) (eqn. 1). Some authors have suggested to use DBH only (Pilli, Anfodillo & Carrer 2006) or DBH and WSG only (Chave *et al.* 2005). We chose to keep all the three variables and to deal explicitly with missing data.

$$\log(AGB_i) = \beta_0 + \beta_1 \log(DBH_i) + \beta_2 \log(H_i) + \beta_3 \log(WSG_i) + \varepsilon_i, \quad \varepsilon_i \sim \mathcal{N}(0, \sigma^2) \quad \text{Eqn. 1}$$

The estimation of AGB for a tree took into account the uncertainties on the AGB model and eventually on the variables DBH, *H*, and WSG. The AGB model was calibrated with a Bayesian method, the values of $\beta_0, \beta_1, \beta_2, \beta_3$ were sampled from their posterior distribution. The values of DBH, *H*, WSG, if they were uncertain, were sampled from distributions resulting from the DBH model, Height model and WSG model defined below. These sampled values were plugged in the AGB model (eqn. 1) to produce samples of the AGB for a tree.

DBH model

Standard AGB estimations are based on census of trees above 10cm DBH (IPCC 2000). To keep this limit consistent between all the inventories, we had to model the DBH distribution:

- For “inventaire papetier”, the DBH values were sampled in each diameter class from an exponential distribution.
- For inventories where DBH were measured only above 15cm or 20cm, the number of trees in the lowest DBH classes was inferred from the forest plot DBH distribution (Supplementary Material).

Height model

For inventories with only DBH measured, tree height values were sampled from a Michaelis-Menten model (eqn. 2). For inventories with only the numbers of trees per diameter class, once DBH values were first sampled.

$$H_i = \frac{\alpha \times DBH_i}{\gamma + DBH_i} \times \varepsilon_i, \quad \varepsilon_i \sim LN(0, \sigma^2) \quad \text{Eqn. 2}$$

This model was used for height-diameter models (Huang, Titus & Wiens 1992). Although this model was not largely used in the ecologist community we found it to perform particularly well in French Guiana (Molto, Rossi & Blanc in press). To account for the spatial variability of the height-diameter relationship (Feldpausch *et al.* 2011), the coefficients α (asymptote) and $\beta = \alpha/\gamma$ were replaced by linear combinations of forest stand structure and environmental variables (Molto *et al.* in

press). The Height-Diameter model was calibrated with a Bayesian method the values of α and γ were sampled from their posterior distribution. The value of DBH, if it was uncertain, was sampled from the distribution resulting from the DBH model. These sampled values were plugged in the Height-Diameter model (eqn. 1) to produce samples of H for the tree.

WSG model

The uncertainty on WSG depends (i) on the determination level of the tree species and (ii) on the accuracy and completeness of the database used for WSG. The WSG values of a tree i in the

$$WSG_{i,s} \sim \mathcal{N}_{[0.15, 1.3]}(\mu_s, \sigma_s^2) \quad \text{Eqn. 3}$$

species s were sampled from the truncated normal model (eqn. 3):

The estimation of WSG for a tree took into account the intra-species WSG variability and the species phylogeny. A hierarchical structure allow for a meaningful estimation of the mean parameter μ_s and variance parameters σ_s^2 even for species with very few measures. The tree WSG values were sampled in the WSG distribution of its species (eqn. 3). If a tree had no identified species or if the tree species WSG is not in the database of WSG, the tree WSG values were sampled in the regional WSG distribution.

Plot AGB model

We estimated the AGB of a plot with the sum of the estimation of the AGB of the trees in the plot (Figure 1):

$$AGB_{plot} = \sum_{i=1}^{N_{tree_{plot}}} AGB_i \quad \text{Eqn. 4}$$

where AGB_i is defined in (eqn. 1). The estimation of the AGB of a plot was obtained numerically with a Monte-Carlo scheme by sampling of values from the model from eqn. 1.

Spatial AGB model

We spatialized the ABG estimation with an ordinary kriging with covariables (Diggle & Ribero Jr. 2006). The trend μ_i at the location i was expressed as a linear combination of the environment variables (Eqn. 5). The environment variables are centered and scaled to allow comparison between the different coefficients:

$$\mu_i = \text{Intercept} + \text{type_forest}_i + \text{geol}_i + \gamma_1 * \log_area_drain_i + \gamma_2 * \text{rainfall}_i + \gamma_3 * \text{DSI}_i + \gamma_4 * \text{TRL}_i + \gamma_5 * \text{alt_hydro}_i \quad \text{Eqn. 5}$$

For the discrete variables RSLC (“type_forest”) and geology (“geol”), one coefficient is associated with each modality. The contrasts were chosen so for each variable the coefficients sum to zero.

The spatial correlation function $\rho(d)$ between two locations separated by a distance d was chosen from the exponential family with a fixed $\kappa = 0.5$ (eqn. 6).

$$\rho(d) = \exp\left(-\left(\frac{d}{\phi}\right)^\kappa\right) \quad \text{Eqn. 6}$$

We allowed the model for a nugget effect τ and the error term is noted σ^2 .

The uncertainties on the AGB plot estimations were taken into account for the spatial prediction with a Monte-Carlo scheme. The model inference and the spatial predictions were performed 100 times with frequentist methods for 100 different samples of the forest plot AGB distributions defined by equation 4. Thus, the uncertainty of the AGB of the census plots was propagated to the spatial predictions, but not the uncertainty of the spatial model parameters γ_j , ϕ , τ , and σ^2 .

The mean map was computed on a 1 km² cells grid as the mean of the 100 predicted mean maps $m_{i_{1:100}}$. The standard deviation map is computed from the 100 predicted variance maps $\sigma^2_{i_{1:100}}$ as:

$$s_i = \sqrt{\sigma^2_{i_{1:100}} + \text{Var}(m_{i_{1:100}})} \quad \text{Eqn. 7}$$

Slope correction

Because the terrain is not flat, the AGB values have to be projected to be represented on a flat map. On field, the data were collected on true terrain surface. First, the map was produced with uncorrected AGB value, the AGB value of each 1 km² pixel representing the AGB attributed to the real terrain area of the pixel. Then, the real area of each 1 km² pixel was computed from the 90m altitude map. With this information, the AGB map was corrected to account for the real terrain surface.

The model inference was performed with the functions of the R (R-Core-Team 2012) package geoR (Ribeiro Jr. & Diggle 2001; Diggle & Ribeiro Jr. 2006).

RESULTS

Variogram model

The spatial AGB model (eqn. 5, 6) adequately catches the empirical variogram (Figure 3). While the nugget effect is very strong ($\tau \approx 18500$, *partial sill* ≈ 25000), the correlation at short distances (10 km) only was significant. The parameters of the spatial correlation model are represented on the figure 4 (lower panel). The error term σ is about 80 Mg.ha⁻¹. The range parameter ϕ is estimated to about 15 km.

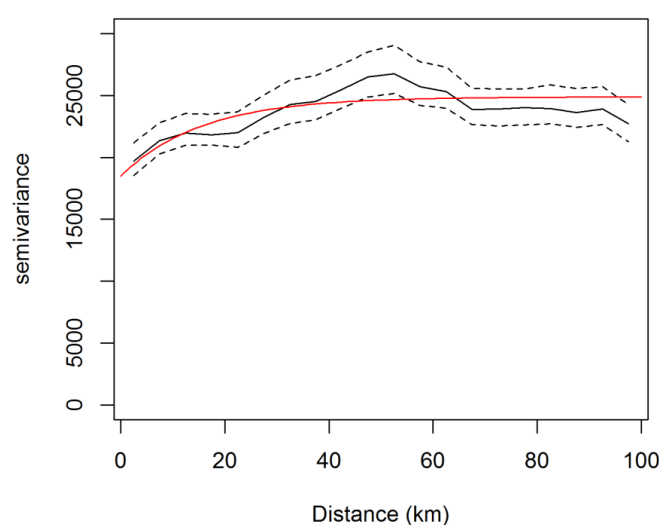


Figure 3: Empirical variogram of the AGB value of the census plots. The envelope does not represent the usual resampling but the uncertainty propagated from the uncertainty of AGB estimations instead. The red line represents the mean of the covariance model.

Spatial trend

The distribution densities of the parameters associated with the trend component of the spatial model (eqn. 6) are presented in the figure 4. The intercept is centered around 440 Mg/ha of fresh AGB.

Some distribution densities of the parameters associated with the trend component of the spatial model (eqn. 5) clearly included 0 in their distribution, *i.e.* the associated variable has no effect on the AGB. It is the case for the hydraulic altitude (“alt_hydro”) and the Terrain Ruggedness Index (TRI). The rainfall and the slope have a clear positive effect on AGB while the dry season index (DSI) and the drained area have a negative effect.

The effect of the different geology classes are also reported in table 1. The recent sediments and the gneiss have a negative effect on biomass (about -20 Mg.ha⁻¹). The granites and gabbros have a positive effect (about +20 Mg.ha⁻¹). The volcanic sediments had no significant effect.

The effect of the different vegetation classes are also reported in table 1. The forest identified as high with regular canopy and (19) and high mixed with open forests (21) had a positive effect on AGB. Low dense forests (18) and forests with disrupted canopy (20) had no effect, while the open/palm forests (22) had a much dispersed negative effect.

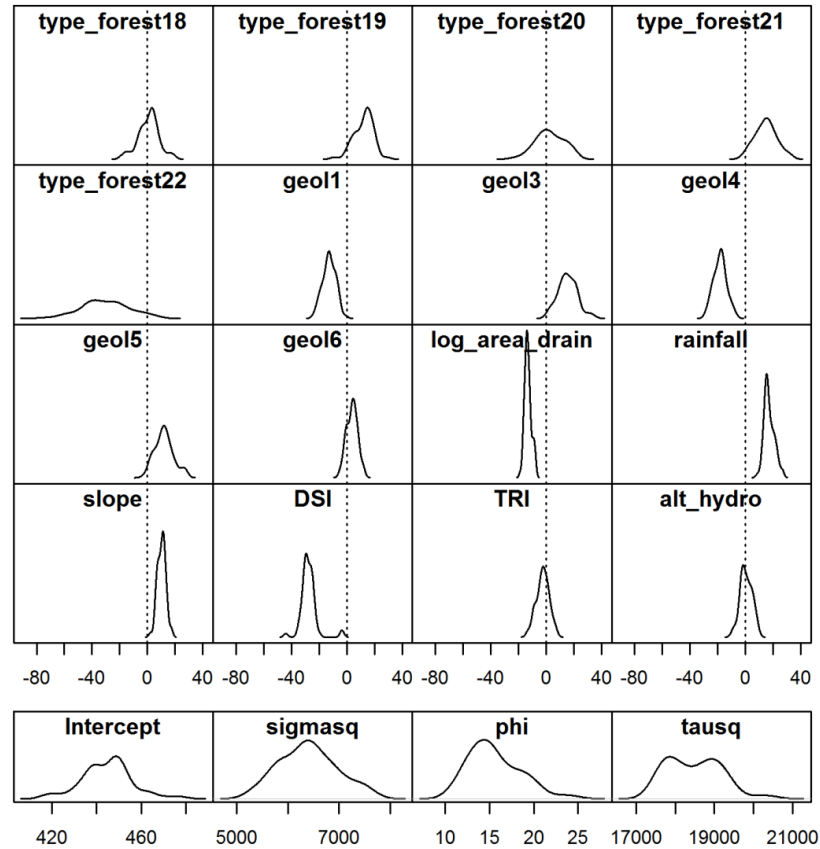


Figure 4: Parameters of the spatial trend and spatial process. The uncertainty is propagated from the uncertainty of AGB forest plots distribution but does not include the uncertainty of the parameters themselves. “type_forest18” to “type_forest22”: vegetation classes described by Gond et al. (2011) (table 1). “geol1” to “geol6”: geology classes (table 1). “sigmasq”, “phi”, and “tausq”: parameters of the spatial correlation model (eqn. 5, 6).

AGB map

The results of spatial predictions are presented with two maps: a mean map and a standard deviation map. The mean map (figure 5) shows particular contrasts where the census plots are located. The AGB standard deviation is lowest at location close to the census plots (figure 6). However this uncertainty decrease is very slight (standard deviation from 140 Mg.ha⁻¹ at the census plots to 165 Mg.ha⁻¹ far from the forest plots).

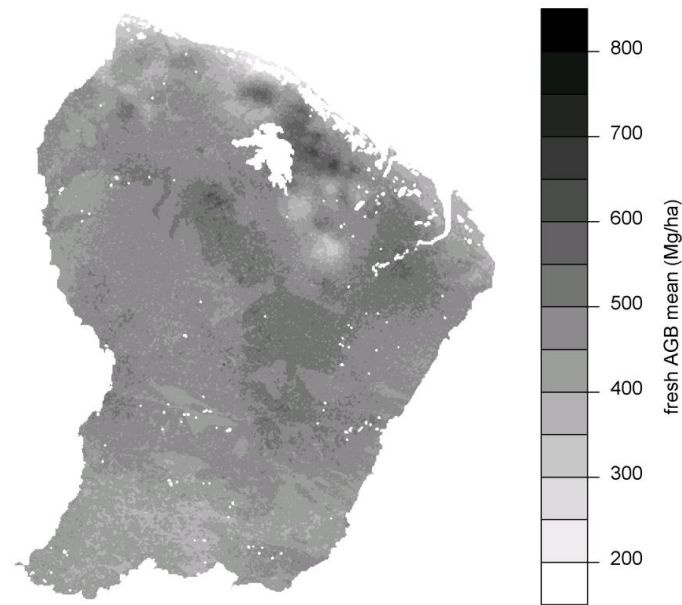


Figure 5: Map of the mean biomass estimation.

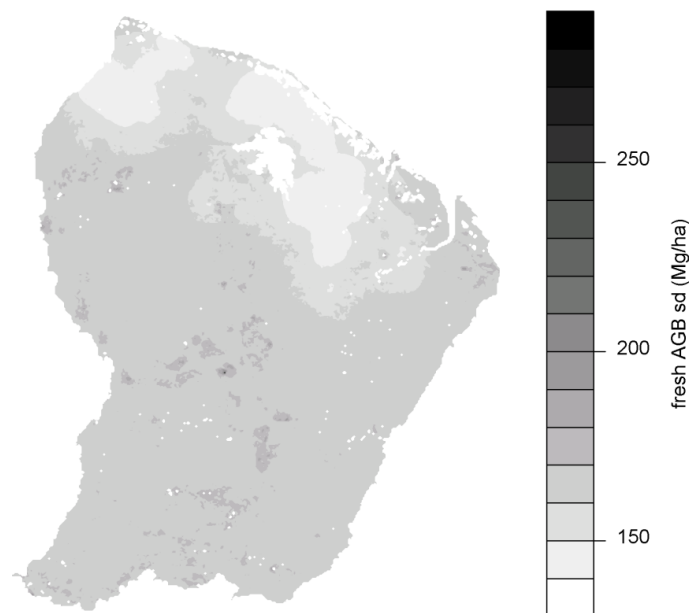


Figure 6: Map of the mean AGB standard deviation. This uncertainty comes from the uncertainty of the AGB of the census plots and the error term of the spatial model. It does not take in account the uncertainty of the parameters of the spatial model. A rough and conservative 95% confidence interval is $[\text{mean} + 2 \cdot \text{sd}, \text{mean} - 2 \cdot \text{sd}]$.

DISCUSSION

Limits of the study

The data were not collected at the same time: trees harvested in 1972, inventories conducted between 1972 and 2012. We hypothesize that the modeled relations did not change during the past 40 years. This may not be true. During the past ten years, punctual climate events impacted the tropical forests (Phillips *et al.* 2009). The increasing CO₂ emissions and the temperature increase may also have increased the carbon stock capacity of the forest (Pan *et al.* 2011). However, the magnitude of the potential error is small compared to the huge errors on our AGB map.

Until the estimation of the AGB of the forest plots, all uncertainties were propagated through Monte-Carlo samples, including the uncertainty of the model parameters inferred with Bayesian methods. However, for computation reasons (too large dataset), the spatial AGB model could not be inferred with Bayesian methods. The parameters of the spatial model were estimated with frequentist optimization methods (Ribeiro Jr. & Diggle 2001). The uncertainties on the spatial model parameters (figure 4) account for the uncertainty of the plot biomass but not for their own uncertainty and the standard deviation map (figure 6) may be slightly underestimated.

From fresh biomass to Carbon

A generic wood Carbon content of 50% is generally assumed (Brown 1997). However, recent studies demonstrated that this empiric value should be refined for precise and unbiased estimations (Lamlom & Savidge 2003; Thomas & Malczewski 2007). The most accurate study for tropical regions is the one of Martin and Thomas (2011). They published Carbon content conversion factor for 59 Panamanian species to estimate the Carbon proportion of oven-dried wood. The mean conversion factor is 47.4%, ranging between species from 41.9 to 51.6 %.

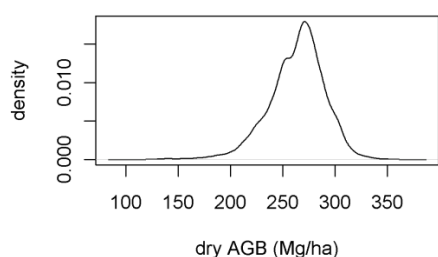


Figure 7: Distribution of dry AGB values in French Guiana.

To be converted into Carbon mass, the forest biomass should be expressed as an oven-dried AGB. The fresh AGB has to be converted to oven-dried AGB thanks to the moisture content. This can be done a priori, measuring moisture content on logged trees during the weighing (Araujo, Higuchi & Junior 1999; Nogueira *et al.* 2008). Because we focused on error propagations, we did not want to correct the fresh mass with an inappropriate moisture content model

and worked with fresh AGB. For comparison with existing studies and eventual conversion to Carbon quantity, we used the same generic moisture content (MC = 42%) Chave *et al.* (2005) used with the same data. This moisture content is a common value in the Amazon basin (Carvalho Jr *et al.* 1995).

Statistical models of wood Carbon and moisture content could be applied to the weighted trees of the tree AGB data and their uncertainties propagated to plot Carbon estimations. Then, the spatial model would handle directly Carbon quantities. This is a required future development to increase the precision of the worldwide carbon estimations.

Comparison with existing values

Common order of magnitude of dry AGB in French Guyana have been reported 300 Mg.ha⁻¹ (Baraloto *et al.* 2011), 310 Mg.ha⁻¹ (Chave, Riera & Dubois 2001), 350Mg.ha⁻¹ (Guitet *et al.* 2006), 375 Mg.ha⁻¹ (Chave *et al.* 2008). The map produced in the present study had slightly smaller values around 265 Mg.ha⁻¹ (figure 7) overall. The slightly higher values in the inventoried area (northern part) are consistent with the previous estimations.

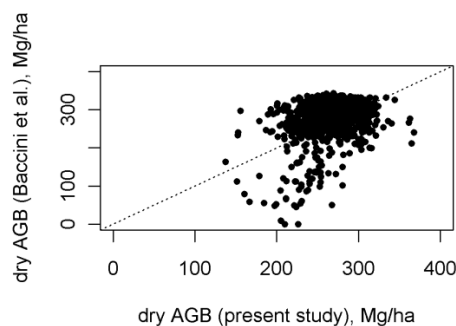


Figure 8: Comparison between our local map and the worldwide map published by Baccini *et al.* (2012) at 2000 random sample location.

Baccini *et al.* (2012) published a worldwide tropical AGB map. We found no correlation between our predicted values and their predicted values (figure 8), but no bias either. The locations where they estimated lower AGB may be places that are not in forest anymore. This will be corrected when our map will be updated with a more recent land- cover map.

WSG spatial variations

The AGB tree model integrated uncertainty of WSG of the logged trees (Molto, Rossi & Blanc in press). This caused the coefficient associated with WSG to contain zero (β_3 in eqn. 1). Thus, we did not develop models for accounting for its spatial variations. However, if the logged trees had had their WSG measured, we would certainly have caught a WSG effect in our AGB tree model (Chave *et al.* 2005). In this case, it would be challenging but interesting to develop a WSG model using environment factors as predictors, maybe linked to the species composition (Fearnside 1997; Chave *et al.* 2006; Flores & Coomes 2011).

Spatial patterns of AGB variation

The most precise environmental variables are computed from the terrain elevation in 90m cells. They describe the topography of the terrain, which has been described as a major determinant for AGB spatial distribution. Through the negative effect of the drained area, we identify the bottom-land plots to have less AGB. This is consistent with the results of Ferry *et al.* (2010) who demonstrated that bottom-lands are associated with a higher mortality, a higher treefall rate, and a lower AGB.

In 1km² cells, Gond *et al.* (2011) interpreted their vegetation classes from 18 to 22 as a gradient of productivity and dynamics (from less to more). They expected the classes 19 and 20 (high canopy forests) to present an equilibrium between turnover and productivity, leading to more AGB. However, we did not find the higher AGB in class 20. The class 18 (low dense forest) is under environment constraints and thus has less AGB. Class 21 is indicated to be more perturbed with higher turnover and less AGB, but we found higher AGB in this class. Gond *et al.* (2011) indicate that the last class denotes very various low-AGB stands; our poorly-estimated negative coefficient confirms this.

At larger scale, high annual rainfall and short dry season are linked to higher AGB (Malhi *et al.* 2006; Quesada *et al.* 2009). This pattern is very clear in our model results. It causes the south locations of the map, drier, to have lower AGBs.

The effects of the geology (table 1) are difficult to interpret because geology does not impact the forest directly. The geological support can affect the soil properties (Bongers *et al.* 2001) that have been found to have an influence on AGB (Paoli, Curran & Slik 2008; Quesada *et al.* 2009; Baraloto *et al.* 2011). The negative effect of recent sediments may have young stands with low AGB. The gneiss (negative effect) may be more fragile than granite and gabbros (positive effects) and cause soil instability. It has also been suggested that different geology could generate different drainage systems (Grimaldi, Grimaldi & Boulet 1990), but we do not know how geology interacts with the topography and hydrology gradient.

Finally, the interpretation of the model coefficients relies mainly on forest dynamics (RSCL classes), itself related to water availability (drained area, rainfall, DSI). However, the relation between rainfall, soils, and water availability is complex (Wagner *et al.* 2011). In addition, the relation between Carbon stock and Carbon dynamics is not straightforward (Malhi *et al.* 2004; Malhi & Wright 2004).

CONCLUSION

In this study, we demonstrated the need to take AGB uncertainty in account when producing AGB maps. While the AGB uncertainty is high at the forest plot level, we successfully identified a spatial correlation process and a spatial trend on environmental gradients. However, the uncertainty is huge and the patterns weak. Satellite methods overcome the search for environmental patterns and treat a physical signal instead, but they do need to take the AGB uncertainty at the forest plot level in account when calibrating their sensors (Dubois-Fernandez *et al.* 2012).

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REFERENCES

- Achard, F., Eva, H.D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T. & Malingreau, J.-P. (2002) Determination of Deforestation Rates of the World's Humid Tropical Forests. *Science*, **297**, 999-1002.
- Araujo, T.M., Higuchi, N. & Junior, J.A.D. (1999) Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Para, Brazil. *Forest Ecology and Management*, **117**, 43-52.
- Asner, G.P., Powell, G.V.N., Mascaro, J., Knapp, D.E., Clark, J.K., Jacobson, J., Kennedy-Bowdoin, T., Balaji, A., Paez-Acosta, G., Victoria, E., Secada, L., Valqui, M. & Hughes, R.F. (2010) High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 16738-16742.
- Baccini, A., Goetz, S.J., Walker, W.S., Laporte, N.T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P.S.A., Dubayah, R., Friedl, M.A., Samanta, S. & Houghton, R.A. (2012) Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change*, **2**, 182-185.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patino, S., Pitman, N.C.A., Silva, J.N.M. & Martinez, R.V. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545-562.
- Baraloto, C., Hardy, O.J., Paine, C.E.T., Dexter, K.G., Cruaud, C., Dunning, L.T., Gonzalez, M.A., Molino, J.F., Sabatier, D., Savolainen, V. & Chave, J. (2012) Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology*, **100**, 690-701.
- Baraloto, C., Paine, C.E.T., Patino, S., Bonal, D., Herault, B. & Chave, J. (2010) Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology*, **24**, 208-216.
- Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B., Davila, N., Mesones, I., Rios, M., Valderrama, E. & Fine, P.V.A. (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677-2688.
- Bock, M., Boehner, J., Conrad, O., Koethe, R. & Ringeler, A. (2004) SAGA GIS. pp. System for Automated Geoscientific Analyses.
- Bongers, F., Charles-Dominique, P., Forget, P.M. & Théry, M. (2001) *Nouragues: dynamics and plant-animal interactions in a Neotropical rainforest*. Springer.
- Brown, S. (1997) Estimating biomass and biomass change of tropical forests: A Primer. *FAO Forestry Paper 134*, pp. 55. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
- Carvalho Jr, J.A., Santos, J.M., Santos, J.C., Leitão, M.M. & Higuchi, N. (1995) A tropical rainforest clearing experiment by biomass burning in the Manaus region. *Atmospheric Environment*, **29**, 2301-2309.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B. & Yamakura, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87-99.
- Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Perez, R. (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 409-420.
- Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Ter Steege, H. & Webb, C.O. (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*, **16**, 2356-2367.
- Chave, J., Olivier, J., Bongers, F., Châtelet, P., Forget, P.-M., van der Meer, P., Norden, N., Riéra, B. & Charles-Dominique, P. (2008) Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology*, **24**, 355-366

- M353 - 310.1017/S0266467408005075.
- Chave, J., Riera, B. & Dubois, M.-A. (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology*, **17**, 79-96.
- Clark, D.B. & Clark, D.A. (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management*, **137**, 185-198.
- Daniel, S., Dubois-Fernandez, P., Le Toan, T., Chave, J., Blanc, L. & Davidson, M. (2010) P-band SAR study of tropical forest in French Guiana. 782400-782400.
- DeFries, R.S., Houghton, R.A., Hansen, M.C., Field, C.B., Skole, D. & Townshend, J. (2002) Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. *Proceedings of the National Academy of Sciences*, **99**, 14256-14261.
- Delor, C., Lahondère, D., Egal, E. & Marteau, P. (2001) Carte géologique de la France à 1:500 000. Département de la Guyane. *Atlas des Départements Français d'Outre-Mer*. BRGM, Orléans.
- Diggle, P.J. & Ribero Jr., P.J. (2006) *Model-based Geostatistics*. Landcaster university, Landcaster, UK.
- Dubois-Fernandez, P., Oriot, H., Coulombeix, C., Cantalloube, H., du Plessis, O.R., Thuy Le, T., Daniel, S., Chave, J., Blanc, L., Davidson, M., Petit, M. & Ieee (2010) *TROPISAR: EXPLORING THE TEMPORAL BEHAVIOR OF P-BAND SAR DATA*.
- Dubois-Fernandez, P.C., Thuy Le, T., Daniel, S., Oriot, H., Chave, J., Blanc, L., Villard, L., Davidson, M.W.J. & Petit, M. (2012) The TropiSAR Airborne Campaign in French Guiana: Objectives, Description, and Observed Temporal Behavior of the Backscatter Signal. *Ieee Transactions on Geoscience and Remote Sensing*, **50**, 3228-3241.
- Fearnside, P.M. (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecology and Management*, **90**, 59-87.
- Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djabbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., Franca, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patino, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodt, F., Sonke, B., Taedoumg, H.E., Tan, S., White, L., Woll, H. & Lloyd, J. (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences*, **8**, 1081-1106.
- Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brien, R.J.W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard C. G.A., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J., Comiskey, J.A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djabbletey, G., Domingues, T.F., Erwin, T.L., Fearnside, P.M., França, M.B., Freitas, M.A., Higuchi, N., C, E.H., Iida, Y., Jiménez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe, D.J., Mitchard, E.T.A., Neill, D.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., Peh, K.S.H., Pena Cruz, A., Peñuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G.M.F., Vásquez, R., Vilanova, E., Vos, V.A., White, L., Willcock, S., Woell, H. & Phillips, O.L. (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, **9**, 3381-3403.
- Ferry, B., Morneau, F., Bontemps, J.-D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**, 106-116.
- Flores, O. & Coomes, D.A. (2011) Estimating the wood density of species for carbon stock assessments. *Methods in Ecology and Evolution*, **2**, 214-220.
- Gibbs, H.K., Brown, S., Niles, J.O. & Foley, J.A. (2007) Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters*, **2**, -.

- Gond, V., Freycon, V., Molino, J.-F., Brunaux, O., Ingrassia, F., Joubert, P., Pekel, J.-F., Prévost, M.-F., Thierron, V., Trombe, P.-J. & Sabatier, D. (2011) Broad-scale spatial pattern of forest landscape types in the Guiana Shield. *International Journal of Applied Earth Observation and Geoinformation*, **13**, 357-367.
- Grimaldi, C., Grimaldi, M. & Boulet, R. (1990) Étude d'un système de transformation sur schiste en Guyane française. *Approches morphologique, géochimique et hydrodynamique. In: Organisation et Fonctionnement des Altérites et des Sols (ed. par IC Wackemlann)(Séminaire ORSTOM 90)*, 81-98.
- Guitet, S., Blanc, L., Chave, J. & Gomis, A. (2006) Expertise sur les références dendrométriques nécessaires au renseignement de l'inventaire national de gaz à effet de serre pour la forêt guyanaise. (ed. M.d.l.A.e.d.l. Pêche).
- Houghton, R.A., Lawrence, K.T., Hackler, J.L. & Brown, S. (2001) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology*, **7**, 731-746.
- Huang, S.M., Titus, S.J. & Wiens, D.P. (1992) Comparison of Nonlinear Height Diameter Functions for Major Alberta Tree Species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestière*, **22**, 1297-1304.
- IPCC (2000) IPCC Good Practice Guidance and Uncertainty Management in National Greenhouse Gas Inventories. Hayama, Kanagawa, Japan.
- Lamblom, S.H. & Savidge, R.A. (2003) A reassessment of carbon content in wood: variation within and between 41 North American species. *Biomass and Bioenergy*, **25**, 381-388.
- Lescure, J.P., Puig, H., Riera, B., Leclerc, D., Beekman, A. & Beneteau, A. (1983) La phytomasse épigée d'une forêt dense en Guyane française. *Acta OEcologica*, **4**.
- Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B. & Lloyd, J. (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 563-591.
- Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A., Salomão, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martínez, R.V. & Vinceti, B. (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107-1138.
- Malhi, Y. & Wright, J. (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **359**, 311-329.
- Martin, A.R. & Thomas, S.C. (2011) A Reassessment of Carbon Content in Tropical Trees. *PloS one*, **6**, e23533.
- Mitchard, E.T.A., Saatchi, S.S., Lewis, S.L., Feldpausch, T.R., Gerard, F.F., Woodhouse, I.H. & Meir, P. (2011) Comment on 'A first map of tropical Africa's above-ground biomass derived from satellite imagery'. *Environmental Research Letters*, **6**, 049001.
- Molto, Q., Herault, B., Boreux, J.-J., Daullet, M., Rousteau, M. & Rossi, V. (in press) Predicting tree height for biomass estimates in tropical forests.
- Molto, Q., Rossi, V. & Blanc, L. (in press) Error propagation for biomass estimation in tropical forests. *Methods in Ecology and Evolution*.
- Nogueira, E.M., Fearnside, P.M., Nelson, B.W., Barbosa, R.I. & Keizer, E.W.H. (2008) Estimates of forest biomass in the Brazilian Amazon: New allometric equations and adjustments to biomass from wood-volume inventories. *Forest Ecology and Management*, **256**, 1853-1867.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S. & Hayes, D. (2011) A Large and Persistent Carbon Sink in the World's Forests. *Science*.

- Paoli, G., Curran, L. & Slik, J. (2008) Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia*, **155**, 287-299.
- Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, Á.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H.t., Stropp, J., Vásquez, R., Zelazowski, P., Dávila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C., E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J. & Torres-Lezama, A. (2009) Drought Sensitivity of the Amazon Rainforest. *Science*, **323**, 1344-1347.
- Pilli, R., Anfodillo, T. & Carrer, M. (2006) Towards a functional and simplified allometry for estimating forest biomass. *Forest Ecology and Management*, **237**, 583-593.
- Ploton, P., Péliissier, R., Proisy, C., Flavenot, T., Barbier, N., Rai, S.N. & Couteron, P. (2011) Assessing aboveground tropical forest biomass using Google Earth canopy images. *Ecological Applications*, **22**, 993-1003.
- Quesada, C.A., Lloyd, J., Schwarz, M., Baker, T.R., Phillips, O.L., Patiño, S., Czimczik, C., Hodnett, M.G., Herrera, R., Arneth, A., Lloyd, G., Malhi, Y., Dezzio, N., Luizão, F.J., Santos, A.J.B., Schmerler, J., Arroyo, L., Silveira, M., Priante Filho, N., Jimenez, E.M., Paiva, R., Vieira, I., Neill, D.A., Silva, N., Peñuela, M.C., Monteagudo, A., Vásquez, R., Prieto, A., Rudas, A., Almeida, S., Higuchi, N., Lezama, A.T., López-González, G., Peacock, J., Fyllas, N.M., Alvarez Dávila, E., Erwin, T., di Fiore, A., Chao, K.J., Honorio, E., Killeen, T., Peña Cruz, A., Pitman, N., Núñez Vargas, P., Salomão, R., Terborgh, J. & Ramírez, H. (2009) Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. *Biogeosciences Discuss.*, **6**, 3993-4057.
- R-Core-Team (2012) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ribeiro Jr., P.J. & Diggle, P.J. (2001) geoR: a package for geostatistical analysis. *R-NEWS*, **1**, 15-18.
- Rutishauser, E., Wagner, F., Hérault, B., Nicolini, E.A. & Blanc, L. (2010) Contrasting above-ground biomass balance in a Neotropical rain forest. *Journal of Vegetation Science*, **21**, 672-682.
- Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M. & Morel, A. (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 9899-9904.
- Sader, S.A., Waide, R.B., Lawrence, W.T. & Joyce, A.T. (1989) Tropical forest biomass and successional age class relationships to a vegetation index derived from landsat TM data. *Remote Sensing of Environment*, **28**, 143-198.
- Sales, M.H., Souza Jr, C.M., Kyriakidis, P.C., Roberts, D.A. & Vidal, E. (2007) Improving spatial distribution estimation of forest biomass with geostatistics: A case study for Rondônia, Brazil. *Ecological Modelling*, **205**, 221-230.
- Sarmiento, C., Patino, S., Paine, C.E.T., Beauchene, J., Thibaut, A. & Baraloto, C. (2011) WITHIN-INDIVIDUAL VARIATION OF TRUNK AND BRANCH XYLEM DENSITY IN TROPICAL TREES. *American Journal of Botany*, **98**, 140-149.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. (2007) IPCC, 2007: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. pp. 996. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Stegen, J.C., Swenson, N.G., Valencia, R., Enquist, B.J. & Thompson, J. (2009) Above-ground forest biomass is not consistently related to wood density in tropical forests. *Global Ecology and Biogeography*, **18**, 617-625.

-
- Thomas, S.C. & Malczewski, G. (2007) Wood carbon content of tree species in Eastern China: Interspecific variability and the importance of the volatile fraction. *Journal of Environmental Management*, **85**, 659-662.
- USGS (2004) Shuttle Radar Topography Mission. (ed. U.o.M. Global Land Cover Facility). College Park, Maryland.
- Vincent, G., Sabatier, D., Blanc, L., Chave, J., Weissenbacher, E., Péliissier, R., Fonty, E., Molino, J.F. & Coueron, P. (2012) Accuracy of small footprint airborne LiDAR in its predictions of tropical moist forest stand structure. *Remote Sensing of Environment*, **125**, 23-33.
- Wagner, F., Herault, B., Stahl, C., Bonal, D. & Rossi, V. (2011) Modeling water availability for trees in tropical forests. *Agricultural and Forest Meteorology*, **151**, 1202-1213.
- Wagner, F., Rossi, V., Stahl, C., Bonal, D. & Herault, B. (2012) Water availability is the main climate driver of neotropical tree growth. *PloS one*, **7**, e34074.
- Wagner, F., Rutishauser, E., Blanc, L. & Herault, B. (2010) Effects of Plot Size and Census Interval on Descriptors of Forest Structure and Dynamics. *Biotropica*, **42**, 664-671.

SUPPLEMENTARY MATERIAL

Supplementary Material 1: from DBH classes to continuous DBH

Instead of sampling each DBH class uniformly, we used an exponential distribution calibrated on the other entire censuses. Again, no particular precision is needed here because the diameter classes are small enough (10cm). We just did want to account for the fact that within a diameter class, high DBH values are less probable than low DBH values.

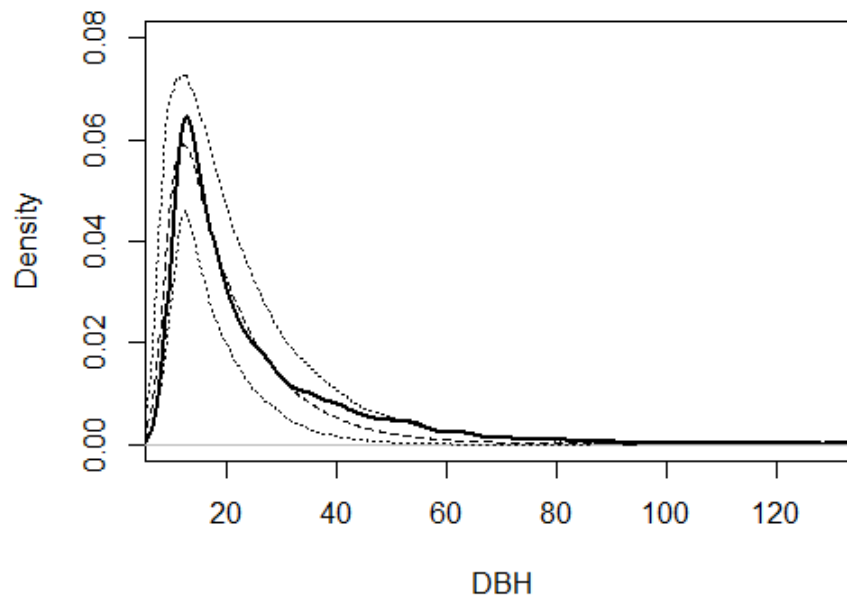


Figure A1: Diameter distribution exponential model. The plain line represents the distribution of the data, the dashed line the prediction median, and the dotted line the 95% confidence interval. Note that the model was only used to sample trees within 10cm large classes of DBH and not to simulate entire forest stands.

Chapitre 6

Conclusion

6.1 Synthèse

À la lecture du dernier chapitre, il apparaît que l'objectif principal de la thèse est bien rempli : nous avons estimé la biomasse d'une forêt tropicale, la Guyane française. Durant tout le processus aboutissant à la carte, nous avons propagé les incertitudes de la façon la plus réaliste et possible. Les choix ont toujours été conservatifs de façon à ne pas sous-estimer l'incertitude et le résultat final doit être lu comme une limite haute de l'incertitude associée à l'estimation de la biomasse.

Nous avons montré que dans les parcelles inventoriées, l'incertitude sur l'estimation de la biomasse vient essentiellement de l'erreur du modèle prédisant la biomasse de chaque arbre. Les modèles de densité de bois et de hauteur d'arbre n'apportent presque pas d'incertitude, en revanche, le modèle de hauteur peut apporter du biais. Le modèle de hauteur peut être amélioré en tenant compte de la variabilité spatiale de la relation hauteur-diamètre. Les parcelles inventoriées ne doivent pas être trop petites (0.1 ha), sinon elles ne sont pas représentatives de la forêt dans laquelle elles sont placées.

La carte finale de biomasse laisse apparaître les forts effets de la composante spatiale du modèle (au nord, près des inventaires) et les faibles effets des covariables environnementales (au sud, loin des inventaires). Les valeurs de biomasse indiquées par la carte, en plus d'avoir une très forte variance, sont donc assujetties aux données de terrain ; or nous avons vu que l'autocorrélation spatiale était très faible. La carte de biomasse moyenne reflète des tendances générales mais ne permet pas d'avoir une estimation de biomasse locale.

6.2 De la biomasse fraîche au carbone

Au cours de la thèse, nous avons choisi de modéliser la biomasse fraîche des arbres, en laissant de côté sa conversion en masse de carbone. Pour obtenir une carte de carbone, il manque deux étapes : la conversion en masse sèche, puis la conversion en masse de carbone.

La proportion de carbone dans le bois est généralement estimée à 50% (Brown, 1997). Cette estimation grossière peut être améliorée (Lamlom & Savidge, 2003; Thomas & Malczewski, 2007; Martin & Thomas, 2011). Lors de la mesure de la proportion de carbone contenu dans un échantillon de bois, l'échantillon est au préalable séché au four à 112°C. Il est donc nécessaire de convertir la biomasse fraîche en biomasse séchée de la même façon.

La meilleure méthode nous semble être de mesurer le taux d'humidité du bois sur des échantillons prélevés sur le terrain au moment de l'abattage de l'arbre. Contrairement à la densité de bois qui est utilisé comme un prédicteur statistique, le taux d'humidité doit être celui de la masse entière de l'arbre, sans biais. Les échantillons doivent donc être prélevés à différentes hauteurs,

différentes profondeur le long du tronc (Araujo *et al.*, 1999b; Nogueira *et al.*, 2008).

Lorsque les mesures de taux d'humidité n'ont pas été réalisées conformément sur le terrain, il est nécessaire d'utiliser un modèle pour prédire ce taux d'humidité. Généralement, des valeurs moyennes sont utilisées (Carvalho Jr *et al.*, 1995; Chave *et al.*, 2005). L'utilisation d'un tel modèle ne permet pas la propagation des incertitudes. Nous pensons que le développement d'un modèle de taux d'humidité, structuré comme le modèle de densité de bois que nous avons développé, permettrait de convertir la biomasse fraîche en biomasse sèche. Ce modèle prendrait en compte les variations inter-spécifiques de taux d'humidité du bois (Muller-Landau, 2004; Williamson & Wiemann, 2010) et permettrait d'estimer la masse sèche des arbres abattus avec une incertitude fiable.

De la même manière, le modèle de proportion de carbone contenu dans la masse de bois sec doit refléter l'incertitude liée au type de bois ou aux différences inter-spécifiques (Lamlom & Savidge, 2003; Thomas & Malczewski, 2007). Il serait aussi possible de développer un modèle structuré comme notre modèle de densité de bois, mais les données semblent trop rares actuellement. Comme les variations inter-spécifiques semblent plutôt faibles (Martin & Thomas, 2011), il est peut-être opportun d'utiliser une distribution globale de teneur en carbone.

Avec des modèles plus sophistiqués qu'une simple moyenne, la masse de carbone est estimée à l'échelle de l'arbre et non pas *a posteriori*. Dans le futur, deux étapes pourront être ajoutées à la calibration d'un modèle de biomasse à l'échelle de l'arbre, correspondant à sa conversion en masse sèche puis en masse de carbone. L'incertitude associé à ces deux modèles devra être propagée et quantifiée. Cela peut se faire de la même manière que celle utilisée au chapitre 3. Le modèle à l'échelle de l'arbre sera alors non pas un modèle de biomasse fraîche

mais un modèle de carbone, et ce sont ensuite des masses de carbone qui seront estimées dans les parcelles inventoriées. L'extrapolation spatiale donnera alors directement une carte de carbone qui aura beaucoup plus de valeur que notre carte de biomasse fraîche dans le cadre du REDD+.

6.3 Précision des estimations de biomasse : quelles améliorations ?

Nous avons vu à deux reprises (chapitre 3 et chapitre 5) que le modèle de biomasse à l'échelle de l'arbre est responsable d'une grande partie de l'incertitude des estimations de biomasse. Comment ce modèle peut-il être amélioré ?

La première piste est l'augmentation du jeu de données. Comme le nombre d'arbres abattus et pesés est finalement assez faible, il pourrait sembler logique que l'ajout de nouveaux arbres améliore le modèle. Cependant, nous avons vu au chapitre 3 que notre modèle de biomasse a le même terme d'erreur que celui de Chave *et al.* (2005). Or notre modèle a été calibré sur une partie des données utilisées par Chave *et al.* (2005). Il semble donc que l'incertitude du modèle soit correctement estimée et corresponde à la variabilité intrinsèque qui existe entre deux arbres de même diamètre, même hauteur, et même densité de bois.

Si peser de nouveaux arbres n'améliorera pas le terme d'erreur du modèle, en revanche, ce serait l'occasion de mettre en œuvre les mesures de densité de bois conformes à notre base de données ainsi que des mesures de taux d'humidité. Abattre et peser des arbres soigneusement choisis reste très intéressant pour mieux comprendre le modèle de biomasse. Les arbres pourraient être choisis pour bien représenter les variabilités d'architectures et de sénescences observées dans la forêt (Poorter *et al.*, 2006).

Pour améliorer le modèle, la solution est peut-être d'ajouter des variables explicatives. Il a été démontré que l'architecture des arbres et leur stade ontogénique influe sur leur biomasse (Rutishauser *et al.*, 2010). L'ajout d'une variable décrivant l'état général de l'arbre et de sa couronne pourrait donc améliorer le modèle. Cependant, un tel modèle doit être calibré, ce qui requiert que la variable supplémentaire soit mesurée sur les arbres abattus. Le nouveau modèle ne pourrait donc pas prendre en compte les anciennes données. Ensuite, le modèle devra être utilisé, ce qui requiert que la variable supplémentaire soit mesurée à grande échelle dans les inventaires forestiers. Le nouveau modèle ne pourrait donc pas être appliqué aux anciens inventaires. De plus, mesurer plus de variables lors de grands inventaires est certainement illusoire.

Pour améliorer les prédictions de biomasse, il serait intéressant de se concentrer sur les gros arbres (plus de 60 cm de diamètre). En effet, un seul arbre peut peser plusieurs dizaines de tonnes (figure 1.5.4). Deux ou trois gros arbres peuvent donc représenter un tiers de la biomasse d'une parcelle de un hectare. C'est l'incertitude associée à l'estimation de ces arbres en particulier qui crée l'incertitude de la biomasse d'une parcelle ; or c'est sur ces arbres que sont les erreurs potentielles sont les plus fortes : arbres creux (Brown & Lugo, 1992; Nogueira *et al.*, 2008), sénescence (Rutishauser *et al.*, 2010), ...

Une autre approche serait d'utiliser les traits fonctionnels. En ce qui concerne la densité de bois, son rôle dans le modèle est logique : elle permet de convertir le volume de l'arbre en masse. Mais comme c'est la seule variable reflétant la variabilité inter-spécifique dans le modèle de biomasse, elle représente en fait bien plus. Si la variabilité inter-spécifique est forte dans le modèle, alors il est peut-être possible de l'expliquer avec d'autres variables estimées à partir de l'identification botanique de l'arbre. Il a déjà été démontré que les certains traits peuvent être

reliés à l'architecture des l'arbre (Poorter *et al.*, 2006) ou à leur croissance (Hérault *et al.*, 2011). Cette approche ne nécessite aucune mesure complémentaire si les nouvelles variables sont incluses dans le modèle de la même façon que la densité de bois.

6.4 Modélisation temporelle

Dans l'introduction, nous avons souligné le fait que les incertitudes permettent des comparaisons spatiales et temporelles de valeurs de biomasses, mais nous n'avons pas développé l'aspect temporel. Notre modèle a été appliqué aux parcelles du dispositif expérimental de Paracou (Gourlet-Fleury *et al.*, 2004) (réseau GUYAFOR) qui sont inventoriées régulièrement (figure 6.4.1).

Encore plus que les mesures spatiales, les mesures temporelles sont autocorrélées et cette structure doit être prise en compte dans le modèle. Appliquer notre modèle à deux inventaires successifs d'une même parcelle est trop conservateur. En effet, lors de la prédiction de la biomasse de la forêt inventoriée l'année 1, des mesures aléatoires de densité de bois et de hauteur sont attribuées à chaque arbre. L'année 2, l'incertitude sur ces mesures est beaucoup plus faible sachant les valeurs de l'année précédente ; il est rare que la hauteur d'un arbre diminue brusquement ou que sa densité de bois varie. Ceci est évidemment valable sur la masse de chaque arbre elle-même.

La modélisation de l'évolution de la biomasse d'une parcelle forestière permanente est donc bien distincte de l'estimation de son stock de biomasse et pourrait être bien plus précise que ce que l'incertitude des estimations du stock laisse supposer. Une première approche naïve serait de contraindre les valeurs de hauteurs, de densités et de biomasse à ne "pas trop" évoluer entre deux années consécutives, le "pas trop" étant représenté par des bornes déterminées arbitrairement

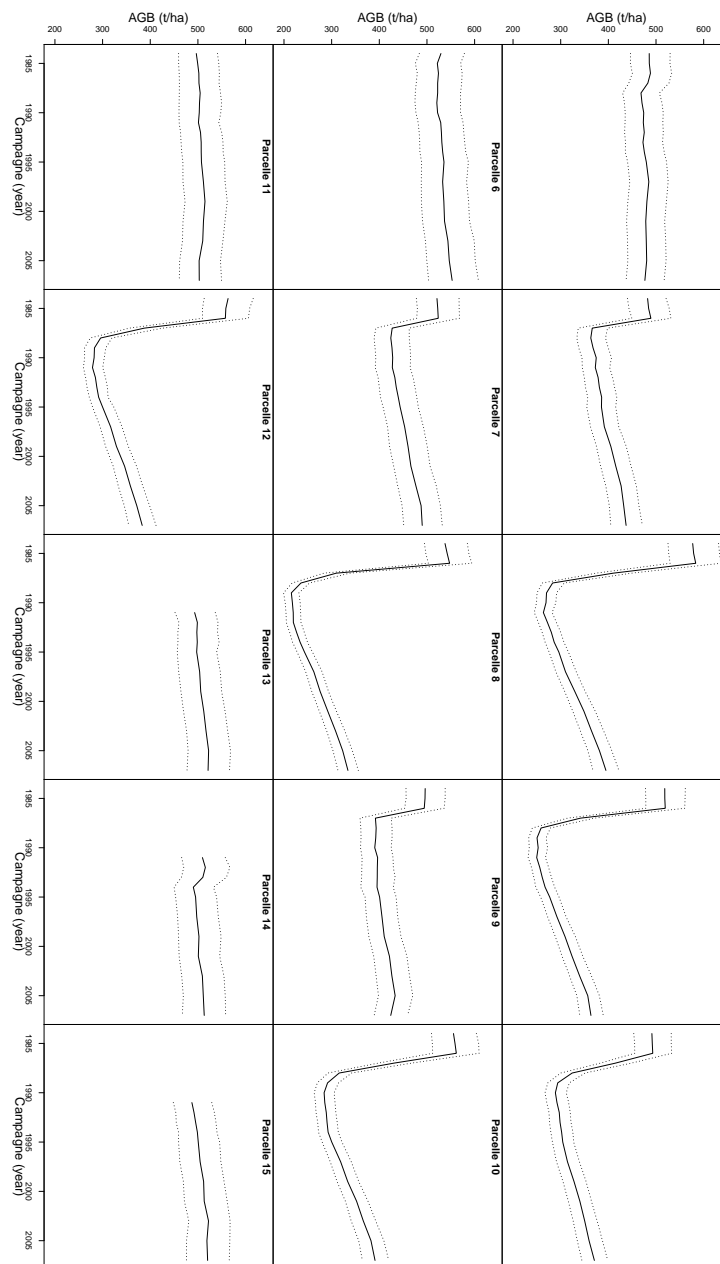


FIGURE 6.4.1 – Évolution de la biomasse dans les parcelles de Paracou. Certaines parcelles ont subi divers niveaux d'exploitation qui se traduit par une perte rapide de biomasse puis une reconstruction progressive. Les parcelles témoin sont les n° 1, 6, 11, 13, 14, 15. Elles sont incluses dans les données d'inventaires utilisées au chapitre 5.

lors des tirages aléatoires la seconde année sachant les valeurs de la première année.

Une autre approche serait d'autocorréler l'erreur pour un même arbre entre les deux années d'inventaire. En effet, un arbre qui a une biomasse plus forte qu'attendu une année, du fait de son architecture par exemple, ne devrait encore avoir une biomasse forte l'année suivante. La difficulté dans ce modèle est de laisser aux arbres la possibilité de brusques chutes de biomasse (perte de plusieurs grosses branches voir du houppier entier).

6.5 Autres services écosystémiques

Dans cette thèse, nous nous focalisons sur le carbone stocké par la forêt, mais les forêts tropicales ont d'autres propriétés qui peuvent être protégées. Il est important de prendre en compte les différents services écosystémiques rendus par un biome pour pouvoir le protéger efficacement. Une politique de conservations basée uniquement sur le carbone est un non-sens (Sangermano *et al.*, 2012). A l'échelle du globe, biomasse et biodiversité sont étroitement liés (Gaston, 2000; Bunker *et al.*, 2005) mais ce n'est pas le cas à l'échelle d'aménagement d'un paysage.

C'est dans ce cadre que dans le chapitre 2 les méthodes d'inventaires ont été analysées sur leurs capacités à mesurer à la fois la biomasse et la biodiversité. Ces deux variables sont souvent estimées à partir des mêmes inventaires forestiers et cela n'est pas toujours adapté (Réjou-Méchain *et al.*, 2011).

En première approche, il peut sembler que la biodiversité ressemble à la biomasse car c'est un service écosystémique qui varie spatialement. Cependant, notre approche de la modélisation de la biomasse est liée à sa nature : une masse par

unité de surface. La biodiversité est un concept beaucoup plus complexe qui ne peut se résumer à un nombre d'espèces par hectare. Si un site présente une grande biodiversité avec des espèces communes, il est moins intéressant qu'un site avec une biodiversité plus faible mais des espèces extrêmement rares. Nos résultats et nos méthodes ne s'appliquent donc pas à la modélisation spatiale de la biodiversité.

Par contre, d'autres services écosystémiques peuvent être modélisés avec une approche similaire à la notre. C'est le cas par exemple du fonctionnement du sol (Ganzeveld *et al.*, 2002; Davidson *et al.*, 2004). Les sols sont en effet des émetteurs ou capteurs potentiels de gaz à effet de serre (oxydes d'azote) et leurs propriétés varient spatialement. L'utilisation de modèles bayésiens et de covariables environnementales permettrait peut-être de cartographier les fonctionnements des sols des forêts tropicales tout en propageant les incertitudes. Cette approche serait d'autant plus intéressante qu'à notre connaissance, les méthodes aériennes ne s'intéressent pas à cette variable.

Annexe

Séparation des effets de la
structure et de l'environnement
sur la biomasse d'un peuplement fo-
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Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests

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Abstract

Tropical forests contain an important proportion of the carbon stored in terrestrial vegetation, but estimated aboveground biomass (AGB) in tropical forests varies two-fold, with little consensus on the relative importance of climate, soil and forest structure in explaining spatial patterns. Here, we present analyses from a plot network designed to examine differences among contrasting forest habitats (terra firme, seasonally flooded, and white-sand forests) that span the gradient of climate and soil conditions of the Amazon basin. We installed 0.5-ha plots in 74 sites representing the three lowland forest habitats in both Loreto, Peru and French Guiana, and we integrated data describing climate, soil physical and chemical characteristics and stand variables, including local measures of wood specific gravity (WSG). We use a hierarchical model to separate the contributions of stand variables from climate and soil variables in explaining spatial variation in AGB. AGB differed among both habitats and regions, varying from 78 Mg ha⁻¹ in white-sand forest in Peru to 605 Mg ha⁻¹ in terra firme clay forest of French Guiana. Stand variables including tree size and basal area, and to a lesser extent WSG, were strong predictors of spatial variation in AGB. In contrast, soil and climate variables explained little overall variation in AGB, though they did co-vary to a limited extent with stand parameters that explained AGB. Our results suggest that positive feedbacks in forest structure and turnover control AGB in Amazonian forests, with richer soils (Peruvian terra firme and all seasonally flooded habitats) supporting smaller trees with lower wood density and moderate soils (French Guianan terra firme) supporting many larger trees with high wood density. The weak direct relationships we observed between soil and climate variables and AGB suggest that the most appropriate approaches to landscape scale modeling of AGB in the Amazon would be based on remote sensing methods to map stand structure.

Keywords: carbon stocks, climate, flooded forest, forest structure, French Guiana, Peru, REDD, soil properties, tropical rainforest, white-sand forest, wood specific gravity

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Introduction

Tropical forests play a vital role in the global carbon cycle, as they comprise approximately 40% of all carbon estimated to be stored in terrestrial vegetation (Houghton, 2005; Malhi *et al.*, 2006). Nevertheless, there remains a large degree of uncertainty in these values, with total estimates of tropical forest biomass carbon stocks ranging from 158 to 324 PgC (Gibbs *et al.*, 2007). The emerging

carbon trading market has underlined the urgent need to improve our understanding of the factors explaining spatial variation in aboveground biomass (AGB) in tropical forests (Gullison *et al.*, 2007), especially given recent escalations in carbon emissions resulting from deforestation, degradation, fire, and drought in tropical regions (Nepstad *et al.*, 1999; Malhi *et al.*, 2008; Phillips *et al.*, 2009). Yet despite some clear global and regional patterns (Malhi *et al.*, 2006; Lewis *et al.*, 2009; Slik *et al.*, 2010), little agreement has been reached regarding the ecological drivers for these patterns and the extent to which they can be extrapolated to construct regional planning maps (Houghton *et al.*, 2001; Gibbs *et al.*, 2007).

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2678 C. BARALOTO *et al.***Table 1** A summary of climate, soil and stand factors observed to explain spatial variation in aboveground biomass in tropical forests. ('+', positive correlation; '-', negative correlation; '*', contrasting reports)

Group	Factor	Effect	References
Climate	Total Precipitation	+	Malhi <i>et al.</i> (2006); Chave <i>et al.</i> (2004)
	Dry season length	–	Malhi <i>et al.</i> (2006); Chave <i>et al.</i> (2004)
Soil	Topography	*	Clark & Clark (2000); Ferry <i>et al.</i> (2010)
	Texture	*	Paoli <i>et al.</i> (2008); Quesada <i>et al.</i> (2009)
	Exchangeable bases	*	Laurance <i>et al.</i> (1999); Quesada <i>et al.</i> (2009)
	Labile P	*	Paoli <i>et al.</i> (2008); Quesada <i>et al.</i> (2009)
	Type	*	DeWalt & Chave (2004)
Stand	Basal area	+	Baker <i>et al.</i> (2004); Malhi <i>et al.</i> (2006); Paoli <i>et al.</i> (2008)
	Density of large trees	+	DeWalt & Chave (2004); Paoli <i>et al.</i> (2008); Rutishauser <i>et al.</i> (2010)
	Mean Tree Height	+	Chave <i>et al.</i> (2005)
	Mean Tree DBH	+	Nelson <i>et al.</i> (1999); Chave <i>et al.</i> (2005)
	Mean Wood specific gravity	*	Baker <i>et al.</i> (2004); DeWalt & Chave (2004); Stegen <i>et al.</i> (2009)

Three groups of explanatory factors have been proposed to explain regional spatial variation of AGB in tropical forests, but to date studies have provided little consensus in their relative contributions (Table 1). Among these, there appears to be concerted evidence for consistent relationships between AGB and rainfall, with moist, stable (short or no dry season) climates supporting the highest biomass in Panama, the Amazon, and Borneo (Chave *et al.*, 2004; Malhi *et al.*, 2006; Quesada *et al.*, 2009; Slik *et al.*, 2010).

Less accord exists among studies examining relationships between AGB of tropical forests and the physical and chemical factors of soils. Several studies have reported positive effects on AGB of soil fertility measures including total nitrogen (N), soil phosphorus, and exchangeable bases (Laurance *et al.*, 1999; DeWalt & Chave, 2004; Paoli *et al.*, 2008), suggesting that AGB may be limited by soil nutrient availability. However, other studies have reported lower biomass on more fertile soils, with higher turnover rates of biomass resulting in lower standing stocks (Van Schaik & Miramanto, 1985; Quesada *et al.*, 2009). Paoli *et al.* (2008) hypothesize that over large gradients in soil fertility, the true relationship with AGB may be hump-shaped, but to date this hypothesis has not been tested explicitly.

A third group of variables proposed to explain spatial patterns in AGB comprises descriptors of forest structure and composition, which we refer to as stand variables. Strong positive correlations may be expected between AGB and variables used in allometric equations, including diameter, height, and wood specific gravity (WSG) (Chave *et al.*, 2005), in addition to metrics of stem density and basal area (Chave *et al.*, 2004). Indeed, strong relationships between AGB and both basal area and large stem density have been found throughout several Neotropical forests (Chave *et al.*, 2004; DeWalt & Chave, 2004; Rutishauser *et al.*, 2010),

and appear to explain the higher AGB estimates for forests of Borneo where larger trees are more frequent (Paoli *et al.*, 2008; Slik *et al.*, 2010). Less agreement has been found for relationships between AGB and wood density. Baker *et al.* (2004) suggested that the east–west gradient in AGB across Amazonia could be explained in large part by gradients of community distributions of wood density. However, Stegen *et al.* (2009) found no consistent relationship between AGB and wood density at different spatial scales across four Neotropical forests.

The overall lack of consensus in tests linking AGB with environmental factors may be explained by three limitations of studies to date, two of which arise in large part from the difficulty of obtaining field data from remote sites. First, few sets of plots exist for which high-quality data are available describing climate, soil properties, and stand variables including species identifications and WSG measures (but see Malhi *et al.*, 2002, 2006). Second, even where these data exist, rarely do plot networks cover broad gradients that can disentangle covariation among climate, soil, forest structure, and other biogeographical factors such as floristic composition. For most lowland terra firme habitats, the east–west gradient in Amazonia represents a concomitant gradient of soil fertility, dry season length, forest turnover, and community wood density, rendering tests of the relative strengths of their relationships with AGB complicated, particularly in plot networks that do not provide replication of soil types across geographic gradients (e.g., Quesada *et al.*, 2009).

Finally, to date stand variables have been treated in the same manner as other environmental descriptors, despite the fact that they are directly or indirectly linked with the allometric calculation of AGB. Therefore, we suggest the most appropriate framework to understanding processes explaining spatial patterns in AGB

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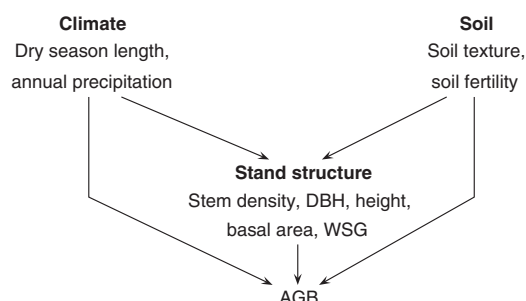


Fig. 1 A conceptual framework for studying the relationships between aboveground biomass (AGB) and stand and environmental descriptors. Previous studies have not addressed the hierarchical nature of these relationships, which results from the direct relationship between stand variables integrated into allometric relationships with AGB.

is hierarchical (Fig. 1). Higher AGB can only be achieved by increases in some stand variable, so this is the necessary first level of any analysis. The key questions then become the extent to which climate and soil explain spatial variation in AGB and the extent to which they explain stand factors which in turn explain spatial patterns in AGB. The response to these questions has important practical implications for how resources should be invested to map AGB at regional scales. If climate and/or soil are significantly correlated with either AGB or the variation in stand structure that explains AGB, then spatial interpolation of these data could be used to map AGB; if they are not, then it would be more appropriate to invest resources in remote sensing methods to map stand structure without integrating environmental data.

In this paper, we evaluate relationships between AGB and climate, soil and stand variables using a new plot network we established across strong climate and soil fertility gradients in two geographic regions of South America. We compile data from 74 plots in Loreto, Peru, and French Guiana that represent the three major lowland rain forest habitat types with contrasting edaphic environments. These three habitats are among the most common habitats in lowland Amazonia, and each has a distinctive flora (Wittman *et al.*, 2006; Fine *et al.*, 2010). First, *terra firme* forests on clay-rich soils are typical of most published studies. Here we include relatively nutrient rich and clay-dominated soils from the Pebas formation in Peru (Hoorn, 1993) in addition to brown sandy soils from Pleistocene river terraces found in Peru (Hoorn, 1993, 1994) and similar sand-silt-clay mixtures from French Guiana (ter Steege, 2000). Second, *seasonally flooded* forests include stands in which the water table is never observed to descend below 60 cm depth and remains at the soil surface for at least two

consecutive months each year (Baraloto *et al.*, 2007; Ferry *et al.*, 2010). In Peru, these include floodplain forests that are inundated during periods of heavy rains (Prance, 1979). Third, *white-sand* forests are characterized by soils with high proportions of sand and little organic material below the surface horizons. They include forests derived from podzols in Peru (Fine *et al.*, 2005; Fine *et al.*, 2010) and French Guiana (Baraloto *et al.*, 2005) as well as quartzites and weathered granite on the margin of inselbergs in French Guiana. This dataset is unique in its experimental design and its quality of data available for climate, soil and stand descriptors, to address the extent to which environment vs. biogeography contribute to spatial patterns of AGB in tropical forests. We use this design to answer three questions.

1. How does AGB vary among habitats, and are these patterns consistent across different geographic regions?
2. Are the relationships between AGB and climate, soil and stand descriptors consistent among habitats and geographic regions?
3. What are the relative contributions of stand and environmental descriptors in explaining spatial patterns of AGB?

Materials and methods

Sampling design

From 2008 to 2010, we sampled 74 stands (forested areas of ca. 20 ha) representing extremes of geographic and environmental gradients, with multiple replicates of the three broad habitat classes described above. Within each geographic region, we selected multiple zones (areas of several thousand hectares, separated by at least 50 km), within which stands corresponding to all three habitats were found (Fig. 2). In Loreto, Peru these included the Allpahuayo-Mishana Reserve in the north, the Jenaro Herrera Center of Investigation and the Matsés Reserved Zone in the south, and the Morona river basin in the west; in French Guiana these included the Laussat Conservation Area in the northwest, the Trinité Reserve in the southwest, the Nouragues Reserve in the southeast, and the Petite Montagne Tortue Conservation Area in the northeast. At each site we established two to six sample plots within different forest stands corresponding to each habitat, with at least 500 m between any two plots. All stands represent lowland forest (<500 m a.m.s.l.) with mature forest subject to natural gap-phase dynamics.

Our plot sample method represents a further modification of the Phillips *et al.* (2003) modified Gentry plots, which we designed to improve AGB estimates. The protocol aggregates ten 10 × 50 m transects within a 2 ha area (for full details, see Appendix S1). This modified 0.5-ha Gentry plot captures a gap and mature phase mosaic well and reduces the risk of sampling bias of a particular phase. Plot sites were placed following substantial prospection in zones selected from topographic

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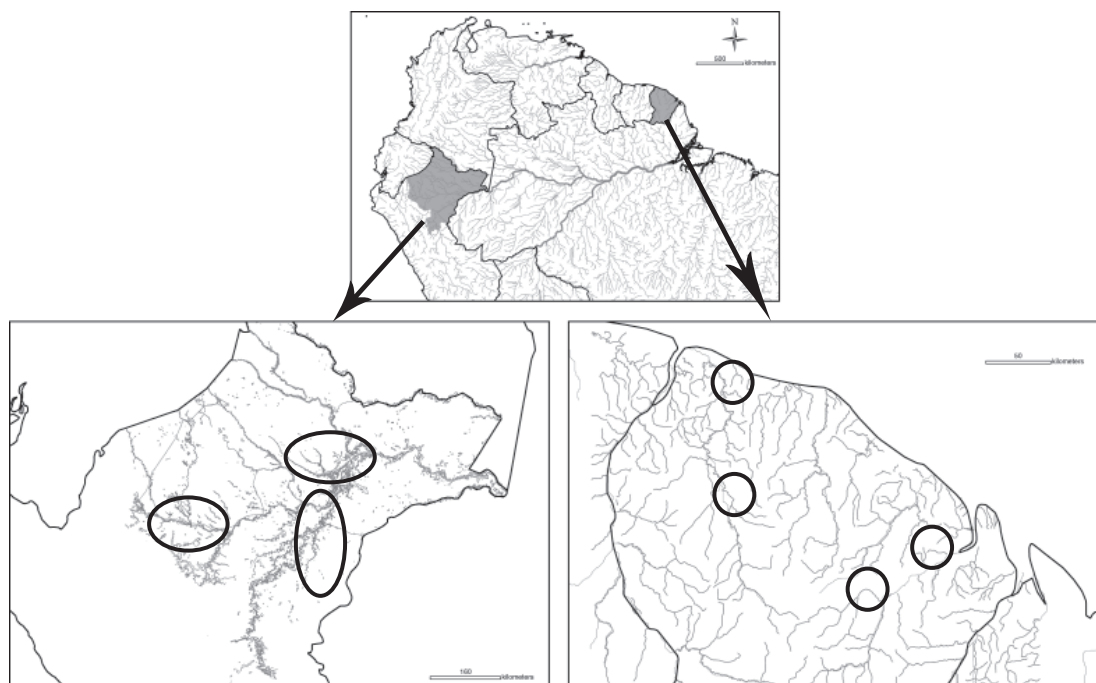


Fig. 2 Map of the Amazon region with major watersheds, illustrating zones where plots were established in Loreto, Peru and French Guiana. Within each of the seven highlighted zones, two to six plots were established in each of three lowland habitat types – seasonally flooded, terra firme clay, or white sand.

maps and satellite imagery where available. The 200×100 m plot perimeter was established to be as representative as possible of the surrounding area (ca. 10–20 ha). UTM coordinates of plots are available upon request.

Links between field and remote sensing estimates of AGB can require slope correction of field estimates to a horizontal plane (Clark & Clark, 2000). We did not correct for slope to create plots with horizontal projection equivalent to 0.5 ha, instead choosing to sample an actual field surface of 0.5 ha. We did, however, measure slope variation among transects using a hand-held clinometer. In all but four of the plots this slope was negligible ($<5^\circ$). In four plots of quartzite white sand in French Guiana, slope values varied between 15° and 27° .

Within each plot, each stem was mapped and its circumference measured to a precision of 2 mm at 1.3 m height (DBH). For stems with irregular trunks or buttresses, circumference was measured (and the point of measure marked with paint) by climbing above irregularities. Tree height was estimated visually by at least two trained persons to arrive at consensus. Visual estimation by members of our crew has been found to provide similar estimates as estimation by laser rangefinders (Figure S1).

Herbarium vouchers were collected for at least one individual of each putative morpho-species in each plot, with all other individuals referenced to this voucher. Taxonomic determinations are still underway; data presented in this paper include determinations to the family level for 99.8% of

stems, to the genus level for 94.6% of stems, to sorted morpho-species for 87.2% of stems, and matches to described species for 65.2% of stems.

Environmental variables

We calculated climatic indices using data from Météo-France in French Guiana and from the IIAP (Instituto de Investigacion de Amazonia Peruana) in Peru, in the meteorological stations nearest to each plot. In cases where weather stations were not located within 10 km of our plots, we used the mean values from any weather stations within a 50 km radius of the plot. The maximum period for which comparable data was available for all sites corresponds to the period from 1998 to 2008.

Two climatic indexes were compiled: a mean annual rainfall (hereafter 'Rain') and a dry season index (DSI). Rain was calculated as a calendar-year average. The DSI from these datasets could be calculated based on daily measurements over 11 years: we therefore calculated dry season length as the maximum number of consecutive days in each calendar year receiving <10 mm of precipitation. We report DSI as the mean value over the 11 years for which data was available from all sites.

Bulked 0–15 cm depth soil cores from each of the 10 subplots were collected and combined into a single 500 g sample that was dried at 25°C to constant mass, sieved to 2 mm, and shipped within 3 months for physical and chemical analyses

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(Table 2) at the University of California, Davis DANR laboratory (for full details on laboratory protocols, see Appendix S1).

Estimating AGB

WSG varies widely within and among both species and sites (Patiño *et al.*, 2009), and error associated with WSG estimation can introduce substantial bias into AGB calculations (Sarmiento *et al.*, 2011). To avoid sampling error that can result from regional database compilation (Baraloto *et al.*, 2010b), we measured wood density directly on at least one individual of each species in each plot from the plot network (see Appendix S1 for full details).

We estimated the AGB of smaller trees with diameter at 1.3 m from the ground (DBH) between 2.5 and 10 cm, including palms, from a single equation modified from the model devised by Hughes *et al.* (1999) for a moist tropical forest of South Mexico (Chave *et al.*, 2004):

$$AGB = \frac{WSG \times e^{(-1.9703 + 2.1166 \times \log(DBH))}}{WSG}$$

We estimated the AGB in trees with DBH > 10 cm, including palms, using allometric formulas that integrate WSG (in g cm³), tree height (*H*, in m) and DBH (in cm) (Chave *et al.*, 2005):

$$AGB = 0.0509 \times WSG \times DBH^2 \times H.$$

We also calculated AGB for trees with DBH > 10 cm using an allometry where height was not integrated, to evaluate any

bias that might be introduced in our estimation of height and choice of allometry (Chave *et al.*, 2005):

$$AGB = WSG \times e^{(-1.499 + 2.148 \times \log(DBH) + 0.207 \times \log(DBH)^2 - 0.0281 \times \log(DBH)^3)}.$$

Estimates using the allometry without height were always greater than those that included the height measure, and the bias was greatest in plots with higher AGB (Figure S1). We chose to present AGB values including height for the remainder of analyses in this study.

To permit eventual comparisons with other studies, we corrected all values to a projected horizontal surface area based on clinometers measures of slope in each plot, and we extrapolated AGB to a per-hectare basis.

Stand variables

We defined seven stand variables describing forest structure that have been linked to spatial variation in AGB (Table 1). Principal among these are basal area, mean WSG by plot, mean DBH by plot, and mean height by plot. We also included stem density in three size classes: number of stems DBH between 2.5 and 10 cm; number of stems DBH between 10 and 30 cm, and number of stems with DBH > 30 cm.

Data analysis

To study the broad patterns of regional and local variation of AGB, two-way ANOVA was used to test for AGB differences

Table 2 Environmental and geographic variables represented by the 74 0.5-ha plots in Peru and French Guiana

Group	Variable	Abbreviation	Mean	Min.	Max.
Climate	Rainfall (mm yr ⁻¹)	Rain	2923	2471	4421
	Dry Season Index (days)	DSI	22.3	15	36.8
Soil	N (%)	N	0.17	0.02	0.76
	C (%)	C	2.34	0.51	13.62
	Carbon : nitrogen	CN	15.1	1.94	28.7
	NO ₃ -N (ppm)	NO3	6.5	0.05	55.2
	Olsen P (ppm)	P	4.6	0.05	28.6
	K (mEq/100 g)	K	0.09	0.01	0.32
	Na (mEq/100 g)	Na	0.05	0.01	0.21
	Ca (mEq/100 g)	Ca	1.24	0.01	19.06
	Mg (mEq/100 g)	Mg	0.44	0.02	3.72
	Sand (%)	Sand	58.4	5.0	99.0
	Silt (%)	Silt	18.9	1.0	60.0
	Clay (%)	Clay	22.7	0.4	69.0
Stand	Basal Area (> 2.5 cm DBH) (m ² ha ⁻¹)	BA	33.0	20.1	56.3
	Stems 2.5–10 cm DBH (ha ⁻¹)	Stems2.5.10	2149	780	5760
	Stems 10–30 cm DBH (ha ⁻¹)	Stems10.30	583	284	1376
	Stems > 30 cm DBH (ha ⁻¹)	Stems.sup30	89	12	188
	Plot mean WSG	WSG	0.64	0.51	0.76
	Plot mean Height (m)	Height	13.4	8.9	17.5
AGB	Plot mean DBH (cm)	DBH	14.5	6.4	22.8
	AGB Stems > 10 cm DBH (Mg ha ⁻¹)	AGBsup10	289.1	78.6	604.9
	AGB Stems 2.5–10 cm DBH (Mg ha ⁻¹)	AGB 2.5.10	10.4	4.4	27.7
	AGB Total (Mg ha ⁻¹)	AGB	299.5	105.5	614.8

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among geographic regions ($n = 2$) and habitats ($n = 3$), with Tukey post-hoc tests to compare group means.

We then investigated the relationships between each environmental variables and AGB in two steps. First, we used multiple factor analysis (MFA; Le *et al.*, 2008) to get an overview of the plots and the variables describing them. MFA is a multivariate ordination method, similar to principal component analysis (PCA), which builds axes of highest variance for different groups of variables (e.g., Baraloto *et al.*, 2010a). The advantage of MFA is that variables are separated into groups each of which is given equal weight in the analysis. In our study, this permitted us to separate stand variables that are clearly related to AGB. In addition, the relative contribution of groups with large numbers of variables is not exaggerated, as would be the case here for soil variables. Finally, MFA allows us to place groups of variables as illustrative to explore their relationships in the ordination without influencing the ordination; here, we placed the AGB group as illustrative. These analyses were conducted using the R language and environment for statistical computing version 2.11.1 (R Core Development Team, 2009), with MFA analyses using the package FACTOMINER (Le *et al.*, 2008).

We used results from the MFA to choose representative variables that represent the largest proportion of orthogonal variation in the dataset. We then employed these variables in two successive modeling approaches to examine the extent to which climate and soil explain spatial variation in stand factors, which in turn explain spatial patterns in AGB. We chose three variables describing stand structure [basal area (BA), stand mean DBH (DBH), and community-weighted mean WSG]; two variables describing climate [DSI and annual precipitation (Rain)]; and three variables describing soil properties [sand content (Sand), nitrate concentration (NO_3) and Olsen-phosphorus concentration (P)].

We first used variance partitioning by means of partial linear regression (Legendre & Legendre, 1998) to examine covariation in the relative contributions of stand, climate and soil variables on AGB. From this, it appears that stand variables alone explain more than 90% of variance, but part of this variance was shared with soil and climate factors. This led us to estimate the importance of soil and climate variables in predicting the forest structure descriptors which, in turn, predict the AGB (Fig. 1). We constrained the stand descriptors to be linear combinations of soil and climate variables, and we used a hierarchical modeling framework to write and infer the following model:

$$\text{AGB}_p = a_0 + a_1 \times \widehat{\text{BA}}_p + a_2 \times \widehat{\text{DBH}}_p + a_3 \times \widehat{\text{WSG}}_p + \varepsilon_{a_p}$$

with $\varepsilon_a \sim N(0, \sigma_a^2)$ and where (i) AGB is the above-ground biomass of plot p , (ii) a_i are the model coefficients and (iii) $\widehat{\text{BA}}$, $\widehat{\text{DBH}}$, $\widehat{\text{WSG}}$ are, respectively, the predicted values of BA, DBH, and WSG using:

$$\begin{aligned} X_p &= \beta_0 + \beta_1 \times \text{DSI}_p + \beta_2 \times \text{Rain}_p + \beta_3 \times \text{NO}_3_p \\ &\quad \beta_4 \times \text{P}_p + \beta_5 \times \text{Sand}_p + \varepsilon_{b_p}, \end{aligned}$$

with $\varepsilon_b \sim N(0, \sigma_b^2)$ and where (i) X was calculated as BA, DBH or WSG data of plot p and (ii) β_i are the model coefficients.

Parameter prior distributions were chosen to be noninformative, so that parameter estimations were driven much by the data and less by the specified prior distributions:

$$a_i \sim N(0, 10^6) \quad \beta_i \sim N(0, 10^6), \text{ and } \sigma_i \sim \text{Gamma}(0.01, 0.01).$$

Markov chain Monte Carlo simulations were performed and Gibbs sampling (Geman & Geman, 1984) was completed in WINBUGS 1.4 (Lunn *et al.*, 2000). For each model, the parameter posterior densities were obtained with 50 000 iterations after a burning step (10 000 iterations).

Results

Geographic and environmental variability of AGB

The 74 plots in our network represent a large proportion of the breadth of variation in climate and soil physical and chemical factors that has been reported for lowland forests across Amazonia (Quesada *et al.*, 2009). The different regional zones represent a two-fold gradient in annual precipitation and dry season length, which varies from nearly aseasonal forests in Loreto, Peru (16 consecutive days < 10 mm) to highly seasonal forests in eastern French Guiana (more than 35 days < 10 mm) (Table 2). Together, these sites represent three broad classes of climate – (i) moderate precipitation ($\sim 2700 \text{ mm yr}^{-1}$) with short dry seasons (< 17 days) (all Peru sites); (ii) moderate precipitation ($\sim 2500 \text{ mm yr}^{-1}$) with long dry seasons (25–36 days) (western French Guiana); and (iii) high precipitation ($> 3500 \text{ mm yr}^{-1}$) with moderate dry seasons (~ 24 days) (eastern French Guiana). In addition, the study sites cover broad gradients of soil texture, soil nitrate concentration, and soil available phosphorus (Table 2).

Across our 74 plots, AGB of stems with $\text{DBH} > 10$ cm varied by a factor of 7.8, from a minimum of 78 Mg ha^{-1} in a white sand forest in northern Loreto, Peru to a maximum of 605 Mg ha^{-1} in a terra firme clay forest of the Trinité Reserve in French Guiana (Fig. 3; Table S1). Forests in French Guiana had nearly twice the average AGB (371 Mg ha^{-1}) of forests in Loreto, Peru (215 Mg ha^{-1}). White sand forests had only about two-thirds the AGB of terra firme and seasonally flooded clay soil forests in both countries; this contrast was particularly pronounced within the French Guianan forests (Fig. 3). Seasonally flooded forests varied remarkably in AGB values, particularly within the French Guianan sites, and we did not detect an overall difference in AGB between flooded and terra firme clay forest soils (Table S1).

The contribution of stems < 10 cm DBH to total AGB was particularly pronounced in white sand forests of both countries, where smaller stems contributed on average about 10% of total AGB (vs. $< 3\%$ in terra firme

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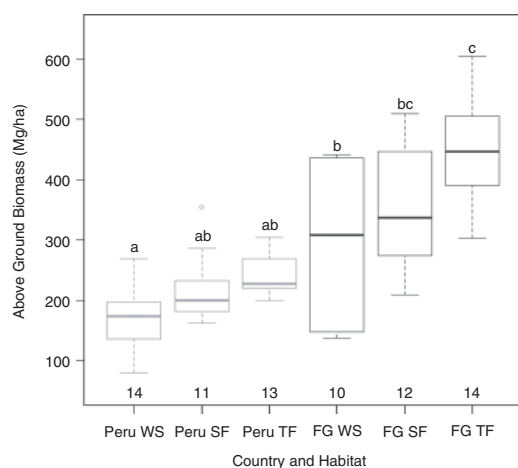


Fig. 3 Boxplot for aboveground biomass of stems >10 cm DBH (Mg ha^{-1}) in different habitats and countries (SF, seasonally flooded; TF, terra firme; WS, white sand). Letters indicate groups with different means following Tukey post-hoc tests. The number of plots represented by each group is indicated at the bottom, with 74 total plots.

clay and seasonally flooded forests; Figure S3). Nevertheless, the overall ranks of countries and habitats remained consistent for total AGB including all stems >2.5 cm DBH (Table S1).

Stand and environmental correlates of AGB

We used MFA to examine the relationships among climate, soil and stand factors in addition to their relationships with AGB. Two major gradients of environmental variation were recovered, explaining 49% of the variance in the dataset. The first MFA dimension has strong loadings of the principal components of the climate group and the forest stand group (Table S2). In particular, it represents a gradient of increasing dry season length, higher annual precipitation, and higher stand basal area (Fig. 4a). The second dimension has strong contributions of both stand and soil variables, opposing infertile sandy soils with high small stem density with fertile clay soils with larger trees (Table S2; Fig. 4a). Mean WSG was tightly positively correlated with soil sand content and soil C:N ratios and tended to increase along the first dimension of climate/geography and to decrease with increasing soil fertility (Dimension 2). Total AGB and AGB of stems with DBH >10 cm were strongly positively correlated with the first dimension.

Ordination of the plots (Fig. 4b) reveals a clear trend of not only geographic separation by climate and stand factors (Dimension 1) but also habitat separation

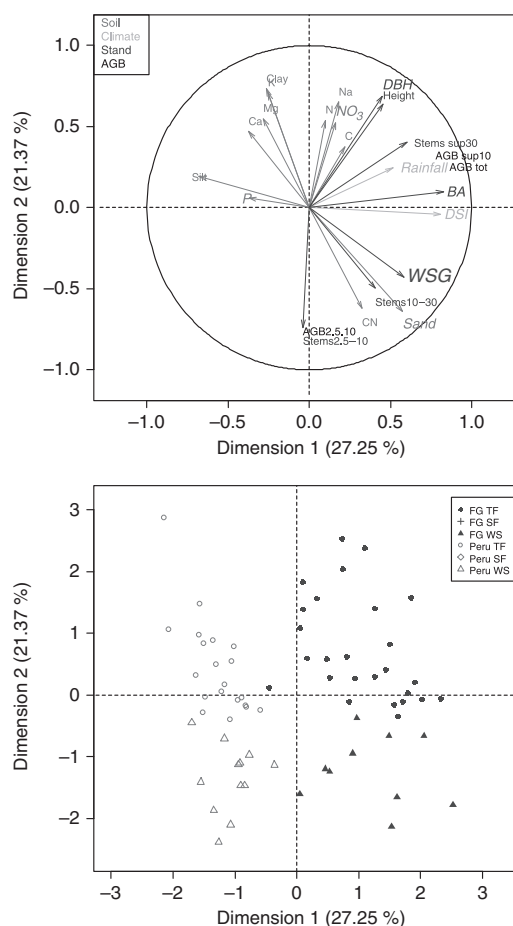


Fig. 4 Ordination of variables and forest plots using multiple factor analysis (MFA), in which aboveground biomass (AGB) variables are used in illustration along the resulting dimensions. The upper panel shows the correlation circle with groups of soil, climate, and stand variables; variables chosen for subsequent analyses are presented in bold. The lower panel shows coordinates of the 74 plots grouped in two geographic regions (Peru, French Guiana) and the three habitat types (terra firme and flooded clay forests, and white-sand forests).

between white-sand vs. clay habitats by soil texture and soil fertility (Dimension 2). Seasonally flooded and terra firme forests do not segregate within the clay-derived soils and can be considered a single group relative to the environmental variables we measured.

Most stand variables showed very strong positive relationships with AGB, confirming the ordination of the MFA analysis (Fig. 4) and the conceptual framework (Fig. 1). Average DBH and basal area were higher in French Guiana than in Peru and generally lowest in white sand forests; whereas community mean WSG was

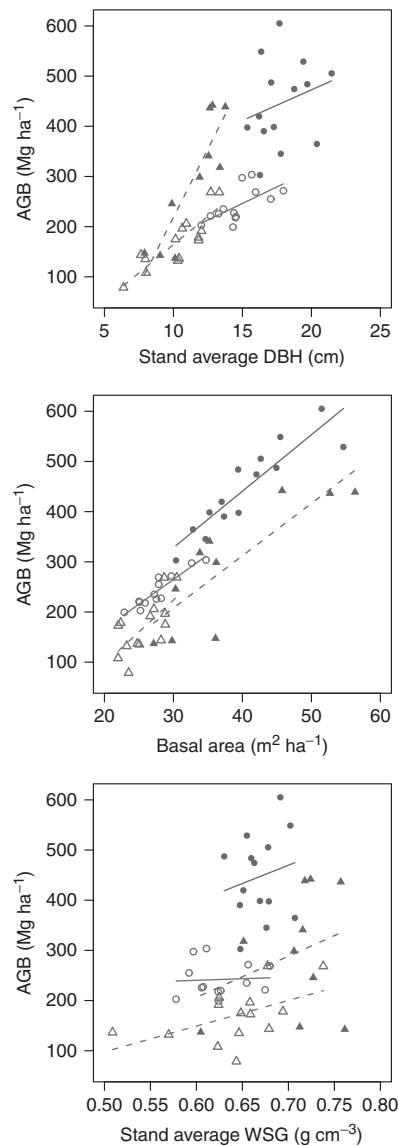
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Fig. 5 Selected relationships between aboveground biomass (AGB) and stand variables. Each panel shows results for 74 plots grouped by geographic region [Peru (open), French Guiana (filled)] and habitat type [white sand (triangles) vs. terra firme and flooded clay forests (circles)]. Shown are slopes from analyses of covariance testing the interaction between forest type and stand variable on AGB.

highest in white-sand forests (Fig. 5). Despite these differences, the general relationship between these stand variables and estimated AGB was strongly congruent. Analysis of covariance revealed very strong effects of both forest type and each stand descriptor

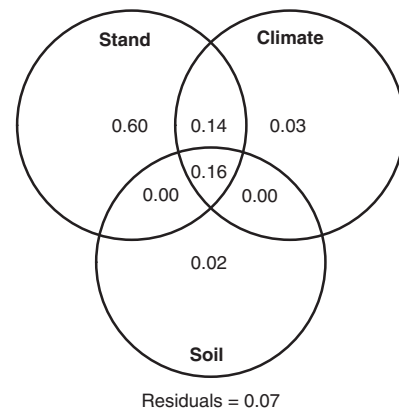


Fig. 6 Venn diagram illustrating the decomposition of spatial variation in AGB between stand, soil and climate variables. Shown are the proportions of variance explained by each combination of variable types. Note that these proportions do not necessarily sum to 1 (Legendre & Legendre, 1998).

on AGB, and the only variation in slope was the stronger slope in the relationship between DBH and AGB in white sand forests of French Guiana (Fig. 5).

The strength of these relationships was confirmed by linear model decomposition, in which 90% of spatial variation in AGB (of 93.5% total) was explained by stand variables alone, with two-thirds of this being independent of soil and climate variables (Fig. 6). Although climate and soil parameters did contribute to explain variation in AGB, this was almost entirely indirectly via covariation with stand parameters.

The Bayesian hierarchical model allowed us to detail the contributions for each climate and soil variable to the variation in stand parameters that explained spatial variation in AGB. Climate variables contributed strongly to the explanatory variation in all three stand descriptors, especially basal area (Fig. 7). Soil texture (percent sand) showed contrasting relationships, with a strong positive relationship with the explanatory variation in WSG and a strong negative relationship with the explanatory variation in stand mean DBH. Soil phosphorus showed negative relationships with the explanatory variation in all three stand descriptors, especially basal area and DBH.

Discussion

Our study provides two important advances to understanding spatial patterns of AGB in Amazonian forests. First, we present clear evidence of contrasting patterns of AGB among broad forest habitat types, in addition to confirming the strong east-west geographic gradient that has been previously described (Fig. 3). Second,

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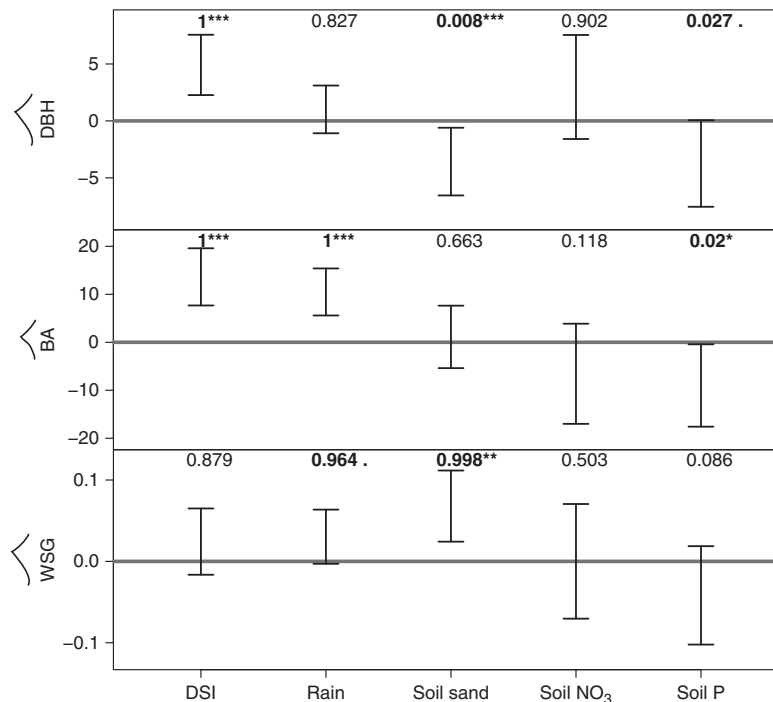


Fig. 7 Results of hierarchical Bayesian model relating five representative climate and soil variables to the variation in aboveground biomass (AGB) explained by three representative stand variables. Shown are the 95% credibility intervals of parameter estimations from the models, with the number indicating the proportion of each distribution which is greater than 0, with significant deviations from 0 shown in bold. Note that the observed values of the predictive variables were standardized to [0, 1] before running the hierarchical model, thus allowing visual comparisons of the coefficients between the predictors. WSG, wood specific gravity; BA, basal area. $P < 0.10$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

despite fine-scale characterization of soil and climate across these broad gradients, we did not uncover strong relationships between any soil or climate variable and AGB (Table 2). Rather, we found compelling evidence for regional and habitat patterns in stand variables describing forest structure and composition (Fig. 4) that were only partly explained by spatial variation in climate and soil physical or chemical properties (Fig. 6). The strength of the arrows in Fig. 1 could be modified to reflect these relationships with a strong arrow between stand variables and AGB; weak arrows between climate and especially soil variables and stand variables; and very weak arrows between climate and soil variables and AGB. Below we discuss these groups of variables in turn and the implications for understanding and modeling regional patterns of AGB in Amazonian forests.

Stand influence on AGB

Our analyses underline the paramount contribution of stand variables to spatial variation in AGB that has been

found in other analyses, and especially the role of larger trees (Chave *et al.*, 2004; DeWalt & Chave, 2004; Rutishauser *et al.*, 2010). This result is not surprising because diameter and height are used to estimate individual tree AGB, as illustrated by the strong linear relation between AGB and basal area (Fig. 5). Large trees (>30 cm DBH) represented 11.4% and 16.7% of Peru and French Guiana tree samples, respectively. French Guianan forests are also characterized by higher total stem densities, especially in terra firme and seasonally flooded forests (Fig. 4); given that these forests also tend to have larger trees, they are characterized by a higher basal area and higher AGB (Fig. 5).

Our study also highlights the importance of smaller stems to carbon stocks, especially in many white-sand habitats. Overall, AGB of stems with DBH between 2.5 and 10 cm varied by a factor of more than five (Table 2), accounting for <1% in some French Guianan terra firme forests to more than 25% of total AGB in a Peruvian white-sand forest (Figure S3). This result contrasts with reports that small trees (<10 cm DBH) account for only 3% of aboveground biomass in French

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Guiana (e.g., Lescure *et al.*, 1983). Eighty percent of biomass estimates in lowland tropical forests are based on measurements of trees >10 cm DBH (Keeling & Phillips, 2007). Our research shows that we should also take small trees into consideration in biomass estimations, particularly in edaphically extreme habitats such as white-sand forests. One reason that most studies may not include small trees is the time required for adequate measurement. We recommend our sampling protocol as particularly efficient to estimate rapidly the total AGB, with an average of 8 person-days to complete field sampling per plot. Still, we note that the allometries for these stems may result in overestimates because they do not include height (cf. Fig. S2), and it would be valuable to revise allometric relationships for smaller stems in future studies.

Baker *et al.* (2004) demonstrate significant differences in stand level WSG for mature forests within Amazonia, with eastern and central forests having 16% denser wood than their western counterparts. In our study, this geographic effect is confirmed, with French Guianan forests having a higher average WSG than Peruvian forests (ANOVA $P < 0.01$). However, this effect was less than half as strong as the effect of habitat (ANOVA $P < 0.001$), with white-sand forests having nearly 20% higher average wood density than terra firme and seasonally flooded forests in both countries (Fig. 5). Across all forests, these patterns explain the weaker positive correlation between WSG and AGB than has been reported in other studies across multiple Amazonian plots (Baker *et al.*, 2004; Quesada *et al.*, 2009). For example, the highest community values of WSG were found in French Guianan white-sand forests, many of which have very low AGB. Moreover, some of the French Guianan terra firme plots with the highest AGB have among the lowest community WSG values (Fig. 5). Although we concur with Baker *et al.* (2004) that patterns of species composition across the Amazon may contribute to differences in AGB because of spatial gradients in community wood density (Ter Steege *et al.*, 2006), we caution against generalizations of positive correlations between WSG and AGB, as this relationship may not be valid across all site comparisons (Stegen *et al.* 2009).

Climate, stand parameters and AGB

Few studies have attempted to relate climate with AGB, perhaps because of limited precision in climate data across tropical forest regions, especially adjacent to permanent vegetation plots. Higher rainfall and/or shorter dry seasons have been linked to higher AGB across Amazonian forests (Malhi *et al.*, 2006; Quesada *et al.*, 2009) and the Isthmus of Panama (Chave *et al.*,

2004). However, these studies could not disentangle the confounding effects of soil and stand composition from those of climate because tropical forests with the combination of high soil fertility, low precipitation and strong seasonality are rare (Quesada *et al.*, 2009). Our study sites included broad gradients of soil fertility and climate regimes (Table 2), and our statistical approach allowed us to examine the covariation among these factors.

We found very strong effects of dry season length on the stand characteristics that explained spatial variation in AGB (Fig. 7), but we note that our plot network does not cover geographic intermediates in Brazil (Fig. 2). Quesada *et al.* (2009) showed that significant correlations between dry season length and AGB dissolved after correcting for spatial autocorrelation among 59 of the RAINFOR terra firme plots. Further investigation combining these databases will be necessary to determine the relative contribution of climatic variables to spatial variation in AGB.

Soil, stand parameters and AGB

Confounding spatial effects similar to those we found with climate can impede analyses of relationships between AGB and soil parameters (Quesada *et al.*, 2009), and this may explain in part the contrasting results reported by previous studies across different spatial scales (Laurance *et al.*, 1999; DeWalt & Chave, 2004; Paoli *et al.*, 2008; Quesada *et al.*, 2009). One of the strengths of our study is the replicated sampling of contrasting soil types at different spatial scales, which reveals several consistent patterns across geographic regions and habitats. Across the entire dataset, as well as within habitats and countries, AGB decreased with increasing soil fertility as defined by Olsen-extracted phosphorus and correlated exchangeable cations (Fig. 4a) because of strong negative correlations between these soil chemical parameters and tree size and basal area (Fig. 7). Nevertheless, nitrate was positively correlated with tree size, perhaps due to accumulation of N over time in the older forests of French Guiana. Overall our results are consistent with the idea that forests on less-weathered soils have higher turnover rates which do not permit accumulation of high AGB, whereas forests on weathered soils may accumulate both standing biomass and soil nitrogen (Russo *et al.*, 2005; Quesada *et al.*, 2009).

Conclusions

Our study has strong implications both for understanding the factors explaining spatial variation in AGB in lowland tropical forests and for modeling AGB in the

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Amazon. We provide sobering news for modelers seeking to use appropriate 'soil and climate functions' to refine estimates of AGB in lowland tropical forests of South America. Unlike in the forests of Borneo (Paoli *et al.*, 2008; Slik *et al.*, 2010), soil appears to exert relatively weak control over AGB across the forests studied here; and climate variables were also poorly correlated with AGB (Fig. 6). On the other hand, our study shows how stand variables may prove to be valuable tools to estimate AGB not only within terra firme forests across geographic regions, but also among contrasting habitats both within and among geographic regions (Fig. 5). Stand variables, especially canopy height, can be derived from remote sensing devices whether radar, lidar or optical (Dubayah *et al.*, 2010; Goetz *et al.*, 2009) and therefore can be used as valuable predictive variables to map and monitor forest biomass over large areas.

The weak relationships we observed between AGB and soil and climate (Fig. 6), despite fine-scale characterization across broad gradients of soil and climate, confirms previous results for little soil nutrient control over AGB in Neotropical forests (DeWalt & Chave, 2004; Quesada *et al.*, 2009). These results are generally consistent with the positive feedback hypothesis (van Schaik & Mirmanto, 1985; Quesada *et al.*, 2009), which contrasts rich soils with high turnover that support fast-growing species with smaller maximum sizes and lower wood density, vs. less fertile soils with lower turnover that support the accumulation of many, larger trees with denser wood. The model works well for both geographic contrasts (Peru vs. French Guiana) and for contrasts between seasonally flooded forests (high turnover) vs. terra firme forests (lower turnover) in the regions studied here (e.g., Ferry *et al.*, 2010) (Fig. 7). We underline the exception reported here for white-sand forests, in which strong oligotrophy and drought stress may favor investment in physical and chemical defenses (Janzen, 1974; Fine *et al.*, 2006) and traits reducing cavitation risk such as high wood density and slow growth (Chave *et al.*, 2009), resulting in the lowest AGB values ever reported (Fig. 3). The integration of forest dynamics data with the intensive measures and plot network design of our study, in collaboration with other plot networks, will permit refined tests of the positive feedback hypothesis in Amazonian forests.

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References

- Baker TR, Phillips OL, Malhi Y *et al.* (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.
- Baraloto C, Goldberg DE, Bonal D (2005) Performance trade offs among tropical seedlings in contrasting microhabitats. *Ecology*, **86**, 2461–2472.
- Baraloto C, Morneau F, Bonal D, Blanc L, Ferry B (2007) Seasonal water stress tolerance and habitat associations within four neotropical tree genera. *Ecology*, **88**, 478–489.
- Baraloto C, Paine CET, Poorter L *et al.* (2010a) Decoupled leaf and stem economics in rainforest trees. *Ecology Letters*, **13**, 1338–1347.
- Baraloto C, Paine TCE, Patino S, Bonal D, Hérault B, Chave J (2010b) Functional trait variation and sampling strategies in species rich plant communities. *Functional Ecology*, **24**, 208–216.
- Chave J, Andalo C, Brown S *et al.* (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**, 87–99.
- Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, **359**, 409–420.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.
- Clark DB, Clark DA (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management*, **137**, 185–198.
- DeWalt SJ, Chave J (2004) Structure and biomass of four lowland Neotropical forests. *Biotropica*, **36**, 7–19.
- Dubayah RO, Sheldon SL, Clark DB, Hofton MA, Blair JB, Hurtt GC, Chazdon RL (2010) Estimation of tropical forest height and biomass dynamics using lidar remote sensing at La Selva, Costa Rica. *Journal of Geophysical Research*, **115**, G00E09, doi: 10.1029/2009JG000933.
- Ferry B, Morneau F, Bontemps JD, Blanc L, Freycon V (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**, 106–116.
- Fine PVA, Daly DC, Villa G, Mesones I, Cameron KM (2005) The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. *Evolution*, **59**, 1464–1478.
- Fine PVA, Garcia-Villacorta R, Pitman N, Mesones I, Kembel SW (2010) A floristic study of the white sand forests of Peru. *Annals of the Missouri Botanical Garden*, **97**, 283–305.
- Fine PVA, Miller ZJ, Mesones I *et al.* (2006) The growth-defense tradeoff and habitat specialization by plants in Amazonian forests. *Ecology*, **87**, S1150–S1162.
- Geman S, Geman D (1984) Stochastic relaxation, Gibbs distributions, and the Bayesian restoration of images. *Transactions on Pattern Analysis and Machine Intelligence*, **6**, 721–741.
- Gibbs HK, Brown S, Niles JO, Foley JA (2007) Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters*, **2**, 045023, doi: 10.1088/1748-9326/2/4/045023.
- Goetz S, Baccini A, Laporte N *et al.* (2009) Mapping and monitoring carbon stocks with satellite observations: a comparison of methods. *Carbon Balance and Management*, **4**, 2.
- Gullison RE, Frumhoff PC, Canadell JG *et al.* (2007) Tropical forests and climate policy. *Science*, **316**, 985–986.
- Hooen C (1993) Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeography Palaeoclimatology Palaeoecology*, **105**, 267–309.

2688 C. BARALOTO *et al.*

- Hoorn C (1994) An environmental reconstruction of the palaeo-Amazon River system (Middle-Late Miocene, NW Amazonia). *Palaeogeography Palaeoclimatology Palaeoecology*, **112**, 187–238.
- Houghton RA (2005) Aboveground forest biomass and the global carbon balance. *Global Change Biology*, **11**, 945–958.
- Houghton RA, Lawrence KT, Hackler JL, Brown S (2001) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. *Global Change Biology*, **7**, 731–746.
- Hughes RF, Kauffman JB, Jaramillo VJ (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology*, **80**, 1892–1907.
- Janzen DH (1974) Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica*, **6**, 69–103.
- Keeling HC, Phillips OL (2007) The global relationship between forest productivity and biomass. *Global Ecology and Biogeography*, **16**, 618–631.
- Laurance WF, Fearnside PM, Laurance SG *et al.* (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management*, **118**, 127–138.
- Le S, Josse J, Husson F (2008) FactoMineR: an R Package for Multivariate Analysis. *Journal of Statistical Software*, **25**, 1–18.
- Legendre P, Legendre L (1998) *Numerical Ecology*. Elsevier, Amsterdam.
- Lescure JP, Puig H, Riera B, Declerc D, Beekman A, Benetau A (1983) La phytomasse épigée d'une forêt dense en Guyane française. *Acta Oecologica*, **4**, 237–251.
- Lewis SL, Lopez-Gonzalez G, Sonke B *et al.* (2009) Increasing carbon storage in intact African tropical forests. *Nature*, **457**, 1003–1006.
- Lunn DJ, Thomas A, Best N, Spiegelhalter D (2000) WinBUGS – A Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325–337.
- Malhi Y, Phillips OL, Lloyd J *et al.* (2002) An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *Journal of Vegetation Science*, **13**, 439–450.
- Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA (2008) Climate change, deforestation, and the fate of the Amazon. *Science*, **319**, 169–172.
- Malhi Y, Wood D, Baker TR *et al.* (2006) The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**, 1107–1138.
- Nelson BW, Mesquita R, Pereira JLG, De Souza SGA, Batista GT, Couto LB (1999) Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *Forest Ecology and Management*, **117**, 149–167.
- Nepstad DC, Verissimo A, Alencar A *et al.* (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, **398**, 505–508.
- Paoli GD, Curran LM, Slik JWF (2008) Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologia*, **155**, 287–299.
- Patño S, Lloyd J, Paiva R *et al.* (2009) Branch xylem density variations across the Amazon Basin. *Biogeosciences*, **6**, 545–568.
- Phillips OL, Aragão LEOC, Lewis SL *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**, 1344–1347.
- Phillips OL, Vargas PN, Monteagudo AL *et al.* (2003) Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology*, **91**, 757–775.
- Prance GT (1979) Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia*, **31**, 26–38.
- Quesada CA, Lloyd J, Schwarz M *et al.* (2009) Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. *Biogeosciences Discuss*, **6**, 3993–4057.
- R Core Development Team (2009). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Russo SA, Davies SJ, King DA, Tan S (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Tropical Ecology*, **93**, 879–889.
- Rutishauser E, Wagner F, Hérault B, Nicolini E, Blanc L (2010) Contrasting above ground biomass balance in a neotropical rain forest. *Journal of Vegetation Sciences*, **21**, 672–682.
- Sarmiento C, Patiño S, Paine CET, Beauchene J, Thibaut A, Baraloto C (2011) Within-individual variation of trunk and branch xylem density in tropical trees. *American Journal of Botany*, **98**, 140–149.
- Slik JWF, Aiba SI, Brearley FQ *et al.* (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography*, **19**, 50–60.
- Stegen JC, Swenson NG, Valencia R, Enquist BJ, Thompson J (2009) Above-ground forest biomass is not consistently related to wood density in tropical forests. *Global Ecology and Biogeography*, **18**, 617–625.
- Ter Steege H (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology*, **16**, 801–828.
- Ter Steege H, Pitman NCA, Phillips OL *et al.* (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, **443**, 444–447.
- Van Schaik CP, Mirmanto E (1985) Spatial variation in the structure and litterfall of a Sumatran rain forest. *Biotropica*, **17**, 196–205.
- Wittman F, Schongart J, Montero JC *et al.* (2006) Tree species composition and diversity in white-water forests across the Amazon Basin. *Journal of Biogeography*, **33**, 1334–1347.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Reliability of visual estimation of tree height.

Figure S2. AGB estimated without height always exceeds estimates integrating height.

Figure S3. Boxplot for aboveground biomass of stems < 10 cm DBH.

Table S1. ANOVA summary of habitat and country effects on AGB.

Table S2. Contributions of environmental variables to the MFA analysis.

Appendix S1. Details of methods.

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References

- Aide, T. Mitchell, Zimmerman, Jess K., Pascarella, John B., Rivera, Luis, & Marcano-Vega, Humfredo. 2000. Forest Regeneration in a Chronosequence of Tropical Abandoned Pastures : Implications for Restoration Ecology. *Restoration Ecology*, **8**(4), 328–338.
- Allen, Craig D., Macalady, Alison K., Chenchouni, Haroun, Bachelet, Dominique, McDowell, Nate, Vennetier, Michel, Kitzberger, Thomas, Rigling, Andreas, Breshears, David D., Hogg, E. H., Gonzalez, Patrick, Fensham, Rod, Zhang, Zhen, Castro, Jorge, Demidova, Natalia, Lim, Jong-Hwan, Allard, Gillian, Running, Steven W., Semerci, Akkin, & Cobb, Neil. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**(4), 660–684. (Ted).
- Araujo, T. M., Higuchi, N., & Junior, J. A. D. 1999a. Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Para, Brazil. *Forest Ecology and Management*, **117**(1-3), 43–52. 180MR Times Cited :44 Cited References Count :9.
- Araujo, T. M., Carvalho, J. A., Higuchi, N., Brasil, A. C. P., & Mesquita, A. L. A. 1999b. A tropical rain-forest clearing experiment by biomass burning in the state of Para, Brazil. *Atmospheric Environment*, **33**(13), 1991–1998. 182QH Times Cited :18 Cited References Count :20.
- Baccini, A., Goetz, S. J., Walker, W. S., Laporte, N. T., Sun, M., Sulla-Menashe,

- D., Hackler, J., Beck, P. S. A., Dubayah, R., Friedl, M. A., Samanta, S., & Houghton, R. A. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate Change*, **2**(3), 182–185. 910JE Times Cited :3 Cited References Count :28.
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Lloyd, J., Monteagudo, A., Neill, D. A., Patino, S., Pitman, N. C. A., Silva, J. N. M., & Martinez, R. V. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**(5), 545–562. 820WY Times Cited :151 Cited References Count :56.
- Baraloto, C., Hardy, O. J., Paine, C. E. T., Dexter, K. G., Cruaud, C., Dunning, L. T., Gonzalez, M. A., Molino, J. F., Sabatier, D., Savolainen, V., & Chave, J. 2012. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. *Journal of Ecology*, **100**(3), 690–701. 923MK Times Cited :1 Cited References Count :111.
- Baraloto, Christopher, Rabaud, Suzanne, Molto, Quentin, Blanc, Lilian, Fortunel, Claire, Herault, Bruno, Davila, Nallarett, Mesones, Italo, Rios, Marcos, Valderrama, Elvis, & Fine, Paul V. A. 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**(8), 2677–2688. Times Cited : 0.
- Blanc, L., Echard, M., Herault, B., Bonal, D., Marcon, E., Chave, J., & Baraloto, C. 2009. Dynamics of aboveground carbon stocks in a selectively logged tropical forest. *Ecological Applications*, **19**(6), 1397–1404.
- Bombelli, Antonio, Avitabile, Valerio, Balzter, Heiko, Luca Belelli Marchesini, Martial Bernoux, Brady, Mihael, Hall, Ron, Hansen, Matthew, Matieu Henry, Martin Herold, Janetos, Anthony, Law, Beverly Elizabeth, Raphaël Manlay, Lars Gunnar Marklund, Olsson, Hakan, Pandey, Devendra,

- Mohamed Saket, Christiane Schmulilius, Sessa, Reuben, Shimabukuro, Yosio Edemir, Valentini, Riccardo, & Wulder, Michael. 2009. *Biomass : assessment report on available methodological standards and guides, GTOS-67*. FAO.
- Brown, S. 1997. *Estimating biomass and biomass change of tropical forests : A Primer*. FAO Forestry Paper 134. Rome, Italy : Food and Agriculture Organization of the United Nations (FAO).
- Brown, S., & Lugo, A.E. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia. Caracas*, **17**(1), 8–18.
- Brown, S., Gillepsie, A.J.R., & Lugo, A.E. 1989. Biomass estimation methods for tropical forests with applications to forestry inventory data. *Forest Science*, **35**, 881–902.
- Bunker, Daniel E., DeClerck, Fabrice, Bradford, Jason C., Colwell, Robert K., Perfecto, Ivette, Phillips, Oliver L., Sankaran, Mahesh, & Naeem, Shahid. 2005. Species Loss and Aboveground Carbon Storage in a Tropical Forest. *Science*, **310**(5750), 1029–1031. 10.1126/science.1117682.
- Carvalho Jr, J. A., Santos, J. M., Santos, J. C., Leitão, M. M., & Higuchi, N. 1995. A tropical rainforest clearing experiment by biomass burning in the Manaus region. *Atmospheric Environment*, **29**(17), 2301–2309.
- Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J. P., Nelson, B. W., Ogawa, H., Puig, H., Riera, B., & Yamakura, T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, **145**(1), 87–99. 963CC Times Cited :98 Cited References Count :56.
- Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Ter Steege, H., & Webb, C. O. 2006. Regional and phylogenetic variation of wood density

- across 2456 neotropical tree species. *Ecological Applications*, **16**(6), 2356–2367.
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**(4), 351–366. 417HR Times Cited :25 Cited References Count :108.
- Chave, Jérôme, Olivier, Jean, Bongers, Frans, Châtelet, Patrick, Forget, Pierre-Michel, van der Meer, Peter, Norden, Natalia, Riéra, Bernard, & Charles-Dominique, Pierre. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology*, **24**(04), 355–366 M3 – 10.1017/S0266467408005075.
- Clark, David B., Clark, Deborah A., & Oberbauer, Steven F. 2010. Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO₂. *Global Change Biology*, **16**(2), 747–759.
- Clark, Deborah A. 2007. Detecting Tropical Forests' Responses to Global Climatic and Atmospheric Change : Current Challenges and a Way Forward. *Biotropica*, **39**(1), 4–19.
- Davidson, E.A., Ishida, F.Y., & Nepstad, D.C. 2004. Effects of an experimental drought on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Change Biology*, **10**(5), 718–730.
- Delor, C., Lahondère, D., Egal, E., & Marteau, P. 2001. *Carte géologique de la France à 1 :500 000. Département de la Guyane.*
- Eggleston, S. 2006. *IPCC guidelines for national greenhouse gas inventories*. Vol. 4. AFOLU (Agriculture, Forestry and Other Land Use), Kanagawa, Japan : Institute for Global Environmental Strategies (IGES). Monograph Wageningen UR Library.

- FAO. 2000. *Global Forest Resources Assessment 2000*. Tech. rept. Organisation des Nations Unies pour l'alimentation et l'agriculture.
- FAO. 2010. *Global Forest Resources Assessment 2010*. Tech. rept. Organisation des Nations Unies pour l'alimentation et l'agriculture.
- Fearnside, Philip M., & Laurance, William F. 2004. Tropical Deforestation And Greenhouse-gas Emissions. *Ecological Applications*, **14**(4), 982–986.
- Feldpausch, T. R., Banin, L., Phillips, O. L., Baker, T. R., Lewis, S. L., Quesada, C. A., Affum-Baffoe, K., Arets, E. J. M. M., Berry, N. J., Bird, M., Brondizio, E. S., de Camargo, P., Chave, J., Djangbletey, G., Domingues, T. F., Drescher, M., Fearnside, P. M., Franca, M. B., Fyllas, N. M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M. O., Iida, Y., Salim, K. A., Kassim, A. R., Keller, M., Kemp, J., King, D. A., Lovett, J. C., Marimon, B. S., Marimon, B. H., Lenza, E., Marshall, A. R., Metcalfe, D. J., Mitchard, E. T. A., Moran, E. F., Nelson, B. W., Nilus, R., Nogueira, E. M., Palace, M., Patino, S., Peh, K. S. H., Raventos, M. T., Reitsma, J. M., Saiz, G., Schrod, F., Sonke, B., Taedoumg, H. E., Tan, S., White, L., Woll, H., & Lloyd, J. 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences*, **8**(5), 1081–1106.
- Flores, O., & Coomes, D. A. 2011. Estimating the wood density of species for carbon stock assessments. *Methods in Ecology and Evolution*, **2**(2), 214–220.
- Foody, Giles M., Palubinskas, Gintautas, Lucas, Richard M., Curran, Paul J., & Honzak, Miroslav. 1996. Identifying terrestrial carbon sinks : Classification of successional stages in regenerating tropical forest from Landsat TM data. *Remote Sensing of Environment*, **55**(3), 205–216.
- Ganzeveld, LN, Lelieveld, J., Dentener, FJ, Krol, MC, Bouwman, AJ, & Roelofs, G.J. 2002. Global soil-biogenic NO_x emissions and the role of canopy processes. *Journal of Geophysical research*, **107**(D16), 4298.

- Gaston, Kevin J. 2000. Global patterns in biodiversity. *Nature*, **405**(6783), 220–227. 10.1038/35012228.
- Gehring, C., Park, S., & Denich, M. 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. *Forest Ecology and Management*, **195**(1), 69–83.
- Gibbs, H. K., Brown, S., Niles, J. O., & Foley, J. A. 2007. Monitoring and estimating tropical forest carbon stocks : making REDD a reality. *Environmental Research Letters*, **2**(4), –.
- Goetz, Scott J., Baccini, Alessandro, Laporte, Nadine T., Johns, Tracy, Walker, Wayne, Kelndorfer, Josef, Houghton, Richard A., & Sun, Mindy. 2009. Mapping and monitoring carbon stocks with satellite observations : a comparison of methods. *Carbon balance and management*, **4**, 2.
- Gond, Valéry, Freycon, Vincent, Molino, Jean-François, Brunaux, Olivier, Ingrasias, Florent, Joubert, Pierre, Pekel, Jean-François, Prévost, Marie-Françoise, Thierron, Viviane, Trombe, Pierre-Julien, & Sabatier, Daniel. 2011. Broad-scale spatial pattern of forest landscape types in the Guiana Shield. *International Journal of Applied Earth Observation and Geoinformation*, **13**(3), 357–367.
- Gourlet-Fleury, S., Guehl, J.M.L, & Laroussinie, O. 2004. *Ecology and management of a neotropical rainforest - lessons drawn from Paracou, a long-term experimental research site in French Guiana*. Elsevier.
- Guitet, S, Blanc, L., Chave, J., & Gomis, A. 2006. *Expertise sur les references dendrométriques nécessaires au renseignement de l'inventaire national de gaz a effet de serre pour la foret guyanaise*.
- Hickler, Thomas, Smith, Benjamin, Prentice, I. Colin, MjÖFors, Kristina, Miller, Paul, Arneth, Almut, & Sykes, Martin T. 2008. CO₂ fertilization in tem-

- perate FACE experiments not representative of boreal and tropical forests. *Global Change Biology*, **14**(7), 1531–1542.
- Houghton, R. A. 2005. Aboveground Forest Biomass and the Global Carbon Balance. *Global Change Biology*, **11**(6), 945–958.
- Houghton, R. A., Lawrence, K. T., Hackler, J. L., & Brown, S. 2001. The spatial distribution of forest biomass in the Brazilian Amazon : a comparison of estimates. *Global Change Biology*, **7**(7), 731–746. 491FL Times Cited :124 Cited References Count :78.
- Hérault, Bruno, Beauchêne, Jacques, Muller, Félix, Wagner, Fabien, Baraloto, Christopher, Blanc, Lilian, & Martin, Jean-Michel. 2010. Modeling decay rates of dead wood in a neotropical forest. *Oecologia*, **164**(1), 243–251.
- Hérault, Bruno, Bachelot, Bénédicte, Poorter, Lourens, Rossi, Vivien, Bongers, Frans, Chave, Jérôme, Paine, C. E. Timothy, Wagner, Fabien, & Baraloto, Christopher. 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology*, **99**(6), 1431–1440.
- Hughes, R. Flint, Kauffman, J. Boone, & Jaramillo, Víctor J. 1999. Biomass, Carbon, and Nutrient Dynamics of Secondary Forests in a Humid Tropical Region of México. *Ecology*, **80**(6), 1892–1907.
- Keeling, Helen C., & Phillips, Oliver L. 2007. The global relationship between forest productivity and biomass. *Global Ecology and Biogeography*, **16**(5), 618–631.
- Körner, Christian. 2004. Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society of London. Series B : Biological Sciences*, **359**(1443), 493–498. 10.1098/rstb.2003.1429.
- Lamlom, S. H., & Savidge, R. A. 2003. A reassessment of carbon content in

- wood : variation within and between 41 North American species. *Biomass and Bioenergy*, **25**(4), 381–388.
- Le Toan, T., Quegan, S., Davidson, M. W. J., Balzter, H., Paillou, P., Papathanassiou, K., Plummer, S., Rocca, F., Saatchi, S., Shugart, H., & Ulander, L. 2011. The BIOMASS mission : Mapping global forest biomass to better understand the terrestrial carbon cycle. *Remote Sensing of Environment*, **115**(11), 2850–2860.
- Lescure, J. P., Puig, H., Riera, B., Leclerc, D., Beekman, A., & Beneteau, A. 1983. La phytomasse épigée d'une forêt dense en Guyane française. *Acta OEcologica*, **4**(3).
- Lewis, Simon L., Lloyd, Jon, Sitch, Stephen, Mitchard, Edward T.A., & Laurance, William F. 2009. Changing Ecology of Tropical Forests : Evidence and Drivers. *Annual Review of Ecology, Evolution, and Systematics*, **40**(1), 529–549.
- Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C. I., Di Fiore, A., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Montoya, L. M. M., Monteagudo, A., Neill, D. A., Vargas, P. N., Patino, S., Pitman, N. C. A., Quesada, C. A., Salomao, R., Silva, J. N. M., Lezama, A. T., Martinez, R. V., Terborgh, J., Vinceti, B., & Lloyd, J. 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**(5), 563–591. 820WY
Times Cited :79 Cited References Count :47.
- Malhi, Yadvinder, & Grace, John. 2000. Tropical forests and atmospheric carbon dioxide. *Trends in Ecology & Evolution*, **15**(8), 332–337.
- Malhi, Yadvinder, Wood, Daniel, Baker, Timothy R., Wright, James, Phillips, Oliver L., Cochrane, Thomas, Meir, Patrick, Chave, Jerome, Almeida, Samuel, Arroyo, Luzmilla, Higuchi, Niro, Killeen, Timothy J., Laurance, Su-

- san G., Laurance, William F., Lewis, Simon L., Monteagudo, Abel, Neill, David A., Vargas, Percy Nuñez, Pitman, Nigel C. A., Quesada, Carlos Alberto, Salomão, Rafael, Silva, JosÉ Natalino M., Lezama, Armando Torres, Terborgh, John, MartÍNez, Rodolfo VÁSquez, & Vinceti, Barbara. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology*, **12**(7), 1107–1138.
- Martin, Adam R., & Thomas, Sean C. 2011. A Reassessment of Carbon Content in Tropical Trees. *PloS one*, **6**(8), e23533.
- Muller-Landau, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, **36**(1), 20–32.
- Muukkonen, P., & Heiskanen, J. 2007. Biomass estimation over a large area based on standwise forest inventory data and ASTER and MODIS satellite data : A possibility to verify carbon inventories. *Remote Sensing of Environment*, **107**(4), 617–624. Times Cited : 39.
- Nogueira, E. M., Fearnside, P. M., & Nelson, B. W. 2008. Normalization of wood density in biomass estimates of Amazon forests. *Forest Ecology and Management*, **256**(5), 990–996. 350XZ Times Cited :5 Cited References Count :54.
- Nogueira, Euler Melo, Nelson, Bruce Walker, & Fearnside, Philip M. 2006. Volume and biomass of trees in central Amazonia : influence of irregularly shaped and hollow trunks. *Forest Ecology and Management*, **227**(2), 14–21.
- Pan, Yude, Birdsey, Richard A., Fang, Jingyun, Houghton, Richard, Kauppi, Pekka E., Kurz, Werner A., Phillips, Oliver L., Shvidenko, Anatoly, Lewis, Simon L., Canadell, Josep G., Ciais, Philippe, Jackson, Robert B., Pacala, Stephen, McGuire, A. David, Piao, Shilong, Rautiainen, Aapo, Sitch, Stephen, & Hayes, Daniel. 2011. A Large and Persistent Carbon Sink in the World's Forests. *Science*.

- Phillips, Oliver L., Malhi, Yadvinder, Higuchi, Niro, Laurance, William F., Núñez, Percy V., Vásquez, Rodolfo M., Laurance, Susan G., Ferreira, Leandro V., Stern, Margaret, Brown, Sandra, & Grace, John. 1998. Changes in the Carbon Balance of Tropical Forests : Evidence from Long-Term Plots. *Science*, **282**(5388), 439–442.
- Phillips, Oliver L., Aragão, Luiz E. O. C., Lewis, Simon L., Fisher, Joshua B., Lloyd, Jon, López-González, Gabriela, Malhi, Yadvinder, Monteagudo, Abel, Peacock, Julie, Quesada, Carlos A., van der Heijden, Geertje, Almeida, Samuel, Amaral, Iêda, Arroyo, Luzmila, Aymard, Gerardo, Baker, Tim R., Bánki, Olaf, Blanc, Lilian, Bonal, Damien, Brando, Paulo, Chave, Jerome, de Oliveira, Átila Cristina Alves, Cardozo, Nallaret Dávila, Czimeczik, Claudia I., Feldpausch, Ted R., Freitas, Maria Aparecida, Gloor, Emanuel, Higuchi, Niro, Jiménez, Eliana, Lloyd, Gareth, Meir, Patrick, Mendoza, Casimiro, Morel, Alexandra, Neill, David A., Nepstad, Daniel, Patiño, Sandra, Peñuela, Maria Cristina, Prieto, Adriana, Ramírez, Fredy, Schwarz, Michael, Silva, Javier, Silveira, Marcos, Thomas, Anne Sota, Steege, Hans ter, Stropp, Juliana, Vásquez, Rodolfo, Zelazowski, Przemyslaw, Dávila, Esteban Alvarez, Andelman, Sandy, Andrade, Ana, Chao, Kuo-Jung, Erwin, Terry, Di Fiore, Anthony, C., Eurídice Honorio, Keeling, Helen, Killeen, Tim J., Laurance, William F., Cruz, Antonio Peña, Pitman, Nigel C. A., Vargas, Percy Núñez, Ramírez-Angulo, Hirma, Rudas, Agustín, Salamão, Rafael, Silva, Natalino, Terborgh, John, & Torres-Lezama, Armando. 2009. Drought Sensitivity of the Amazon Rainforest. *Science*, **323**(5919), 1344–1347.
- Pilli, R., Anfodillo, T., & Carrer, M. 2006. Towards a functional and simplified allometry for estimating forest biomass. *Forest Ecology and Management*, **237**(1-3), 583–593. 122MK Times Cited :13 Cited References Count :70.
- Poorter, Lourens, Bongers, Laurent, & Bongers, Frans. 2006. Architecture of 54

- moist-forest tree species : traits, trade-offs, and functional groups. *Ecology*, **87**(5), 1289–1301.
- Ribeiro Jr., P.J., & Diggle, P.J. 2001. geoR : a package for geostatistical analysis. *R-NEWS*, **1**(2), 15–18.
- Réjou-Méchain, M., Fayolle, A., Nasi, R., Gourlet-Fleury, S., Doucet, J.L., Gally, M., Hubert, D., Pasquier, A., & Billand, A. 2011. Detecting large-scale diversity patterns in tropical trees : Can we trust commercial forest inventories ? *Forest Ecology and Management*, **261**(2), 187–194.
- Rutishauser, E., Wagner, F., Herault, B., Nicolini, E. A., & Blanc, L. 2010. Contrasting above-ground biomass balance in a Neotropical rain forest. *Journal of Vegetation Science*, **21**(4), 672–682.
- Sabine, CL, Heinmann, M, Artaxo, P, Bakker, DCE, Chen, CTA, Field, CB, Gruber, N, Le Guéré, C, Prinn, RG, Richey, JE, Lankao, PR, Sathaye, JA, & Valentini, R. 2004. *The Global Carbon Cycle. Integrating Humans, Climate and the Natural World*. SCOPE.
- Sangermano, F., Toledano, J., & Eastman, J.R. 2012. Land cover change in the Bolivian Amazon and its implications for REDD+ and endemic biodiversity. *Landscape ecology*, 1–14.
- Sarmiento, C., Patino, S., Paine, C. E. T., Beauchene, J., Thibaut, A., & Baraloto, C. 2011. Within-individual variation of trunk and branch xylem density in tropical trees. *American Journal of Botany*, **98**(1), 140–149.
- Sharma, Mahadev, & Parton, John. 2007. Height diameter equations for boreal tree species in Ontario using a mixed-effects modeling approach. *Forest Ecology and Management*, **249**(3), 187–198.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., & Miller, H.L. 2007. *IPCC, 2007 : Contribution of Working Group I to*

- the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, United Kingdom and New York, NY, USA : Cambridge University Press.
- Sukhdev, P, Prabhu, R, Kumar, P, Bassi, A, Patwa-Shah, W, Enters, T, Labbate, G, & Greenwalt, J. 2012. *UN-REDD Policy Brief : REDD+ and the Green Economy : Opportunities for a mutually supportive relationship*. Tech. rept. UN-REDD Programme.
- Sun, Guoqing, Ranson, K. Jon, Guo, Z., Zhang, Z., Montesano, P., & Kimes, D. 2011. Forest biomass mapping from lidar and radar synergies. *Remote Sensing of Environment*, **115**(11), 2906–2916. Times Cited : 2 Si.
- Tanner, E. V. J. 1980. Studies on the biomass and productivity in a series of montane rain forests in jamaica. *Journal of Ecology*, **68**(2), 573–588. Times Cited : 85.
- Thomas, S. C., & Malczewski, G. 2007. Wood carbon content of tree species in Eastern China : Interspecific variability and the importance of the volatile fraction. *Journal of Environmental Management*, **85**(3), 659–662.
- Vieilledent, G., Vaudry, R., Andriamanohisoa, S. F. D., Rakotonarivo, O. S., Randrianasolo, H. Z., Razafindrabe, H. N., Rakotoarivony, C. Bidaud, Ebeling, J., & Rasamoelina, M. 2011. A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. *Ecological Applications*, **22**(2), 572–583.
- Vincent, G., Sabatier, D., Blanc, L., Chave, J., Weissenbacher, E., Pélissier, R., Fonty, E., Molino, J. F., & Coutron, P. 2012. Accuracy of small footprint airborne LiDAR in its predictions of tropical moist forest stand structure. *Remote Sensing of Environment*, **125**(0), 23–33.
- Williamson, G. B., & Wiemann, M. C. 2010. Measuring wood specific gravity ... correctly. *American Journal of Botany*, **97**(3), 519–524.