Journal of Ecology

British Ecological Society

Journal of Ecology 2016, **104**, 703–715 doi: 10.1111/1365-2745.12548

Bioclimatic envelope models predict a decrease in tropical forest carbon stocks with climate change in Madagascar

Ghislain Vieilledent[1]*, Oliver Gardi[2,3], Clovis Grinand[4], Christian Burren[5], Mamitiana Andriamanjato[6], Christian Camara[7], Charlie J. Gardner[8,9], Leah Glass[10], Andriambolantsoa Rasolohery[11], Harifidy Rakoto Ratsimba[12], Valéry Gond[1] and Jean-Roger Rakotoarijaona[13]

[1]Cirad – UPR BSEF, F-34398 Montpellier, France; [2]Helvetas Swiss Intercooperation – BP 3044, 101 Antananarivo, Madagascar; [3]Bern University of Applied Sciences – HAFL, CH-3052 Zollikofen, Switzerland; [4]ETC Terra, F-75020 Paris, France; [5]Wildlife Conservation Society, Soavimbahoaka, 101 Antananarivo, Madagascar; [6]Ministère de l'Environnement et des Forêts – Direction Générale des Forêts, 101 Antananarivo, Madagascar; [7]Missouri Botanical Garden, BP 3391, 101 Antananarivo, Madagascar; [8]WWF – Madagascar and Western Indian Ocean Programme Office, BP 738, 101 Antananarivo, Madagascar; [9]School of Anthropology and Conservation, University of Kent – Durrell Institute of Conservation and Ecology, Canterbury, Kent, UK; [10]Blue Ventures – Blue Forests program, Ambanja, Madagascar; [11]Conservation International – Africa and Madagascar Field Division, 101 Antananarivo, Madagascar; [12]Université d'Antananarivo – Département des Eaux et Forêts, BP 175, 101 Antananarivo, Madagascar; and [13]ONE, Antaninarenina, BP 822, 101 Antananarivo, Madagascar

Summary

1. Recent studies have underlined the importance of climatic variables in determining tree height and biomass in tropical forests. Nonetheless, the effects of climate on tropical forest carbon stocks remain uncertain. In particular, the application of process-based dynamic global vegetation models has led to contrasting conclusions regarding the potential impact of climate change on tropical forest carbon storage.

2. Using a correlative approach based on a bioclimatic envelope model and data from 1771 forest plots inventoried during the period 1996–2013 in Madagascar over a large climatic gradient, we show that temperature seasonality, annual precipitation and mean annual temperature are key variables in determining forest above-ground carbon density.

3. Taking into account the explicative climate variables, we obtained an accurate ($R^2 = 70\%$ and RMSE = 40 Mg ha^{-1}) forest carbon map for Madagascar at 250 m resolution for the year 2010. This national map was more accurate than previously published global carbon maps ($R^2 \leq 26\%$ and RMSE $\geq$ 63 Mg ha^{-1}).

4. Combining our model with the climatic projections for Madagascar from 7 IPCC CMIP5 global climate models following the RCP 8.5, we forecast an average forest carbon stock loss of 17% (range: 7–24%) by the year 2080. For comparison, a spatially homogeneous deforestation of 0.5% per year on the same period would lead to a loss of 30% of the forest carbon stock.

5. *Synthesis.* Our study shows that climate change is likely to induce a decrease in tropical forest carbon stocks. This loss could be due to a decrease in the average tree size and to shifts in tree species distribution, with the selection of small-statured species. In Madagascar, climate-induced carbon emissions might be, at least, of the same order of magnitude as emissions associated with anthropogenic deforestation.

Key-words: carbon storage, climate change, deforestation, Madagascar, MODIS, plant–climate interactions, REDD+, species shifting, tree height, tropical forest

*Correspondence author: E-mail: ghislain.vieilledent@cirad.fr

Introduction

Carbon sequestration by tropical forests plays an important role in the regulation of atmospheric CO_2 and global climate change (Houghton 2005; Pan *et al.* 2011). The current carbon stock in the world's forests is estimated to be 861 ± 66 Pg C (1 Pg = 10^{15} g), with 55% of this carbon (471 ± 93 Pg C) being stored in tropical forests (Pan *et al.* 2011). Tropical anthropogenic deforestation is thus responsible for a considerable proportion (6–17%) of global carbon dioxide emissions that affect climate change (van der Werf *et al.* 2009). While the effect of anthropogenic tropical deforestation on carbon dioxide emissions and climate change has been intensively studied in recent years and is recognized as a global issue (Bonan 2008; van der Werf *et al.* 2009; Vieilledent, Grinand & Vaudry 2013b), the effect of climate change on tropical forest carbon storage, leading to a carbon-cycle feedback, remains largely uncertain (Sitch *et al.* 2008; IPCC, 2014).

A major part of the scientific studies dealing with this potential carbon-cycle feedback in tropical forest have used dynamic global vegetation models (DGVMs) coupled to global climate models (GCMs). DGVMs are process-based models which focus on the physiological response of vegetation (through photosynthesis and respiration) to increasing atmospheric CO_2 concentration and changes in temperature and precipitation (Prentice *et al.* 2007). DGVMs generally agree that net primary productivity and carbon storage on land will increase as a result of the simultaneous enhancement of plant photosynthesis and water-use efficiency under higher atmospheric CO_2 concentrations, but will decrease due to higher plant respiration rates associated with warming temperatures (Cox *et al.* 2013). Despite the numerous efforts made to improve DGVMs, large uncertainties remain in the predictions (Cramer *et al.* 2004; Quillet, Peng & Garneau 2010; Adams *et al.* 2013; Scheiter, Langan & Higgins 2013; IPCC, 2014). For instance, Cox *et al.* (2013) reported a range of 330 PgC in the projected change in the amount of carbon stored on tropical land by 2100 and Sitch *et al.* (2008) reported that cumulative land uptake differs by 494 PgC among DGVMs over the 21st century, which corresponds to 50 years of anthropogenic emissions at current level. In the past, DGVMs have either predicted a dieback of tropical forests (Cox *et al.* 2000; Sitch *et al.* 2008), with, for example, a decrease of 30% (from 568 PgC in 2000 to 398 PgC in 2100) of the carbon stored on land under the IPCC (Intergovernmental Panel on Climate Change) business-as-usual scenario IS92a (Cox *et al.* 2000) or a resilience of tropical forests to climate change (Sitch *et al.* 2008; Huntingford *et al.* 2013), with, for example, an average increase of 18% (from 165 Mg ha^{-1} in 1980 to 195 Mg ha^{-1} in 2100) of the African tropical forest carbon stock under IPCC business-as-usual scenario SRES A2 (Huntingford *et al.* 2013). In a study testing five DGVMs predictions of carbon fluxes using measurements of Amazon forests subjected to experimental drought, Powell *et al.* (2013) showed that the majority of models (four out of five) predicted negligible reductions in above-ground biomass in response to drought, which was in contrast to an observed *c.* 20% reduction in forest. Most of the uncertainty around DGVMs predictions is associated with the uncertain response of terrestrial vegetation to climate, that is to drought and heat stress (Sitch *et al.* 2008; Cox *et al.* 2013). DGVMs typically use a limited number of generic plant functional types (PFTs) to describe vegetation. This number is usually low to facilitate model parametrization, but consequently, PFTs might not be representative of the high diversity of tree species and functioning that can be found in the world tropical dry and moist forests (Powell *et al.* 2013; Schimel *et al.* 2015). Improving DGVMs is a difficult task limited by the complexity of the physiological and ecological processes explaining vegetation dynamics (Quillet, Peng & Garneau 2010; Scheiter, Langan & Higgins 2013) and by the limited amount of biological data available for model parametrization (Adams *et al.* 2013; IPCC, 2014). The question of knowing whether tropical forests are likely to compensate for anthropogenic carbon dioxide emissions through a strong positive biomass response to climate change thus remains unanswered.

In contrast to process-based approaches, simpler correlative methods could offer rapid and robust alternatives for the projection of the effects of climate change on tropical forest carbon storage. Despite known limitations (including the fact that they usually do not take into account biotic interactions, species adaptation and dispersal ability, see Pearson & Dawson (2003)), bioclimatic envelope models have been widely used to project the effect of climate change on biodiversity at both the species (Guisan & Zimmermann 2000; Thuiller *et al.* 2005; Vieilledent *et al.* 2013a) and biome level (Hannah *et al.* 2008; Zelazowski *et al.* 2011). For instance, Zelazowski *et al.* (2011) predicted a forest retreat in Amazonia, Central America and parts of Africa, and expansion in other regions, in particular around the Congo Basin. If one of the biological mechanisms explaining the impact of climate change on forest carbon stocks is the direct effect of climate on tree species metabolic rates and forest net primary productivity (Huxman *et al.* 2004; Cox *et al.* 2013), another mechanism that has to be considered on a larger time scale is the shift in tree species relative abundance and tree species range associated with climate change (Iverson & Prasad 1998; Feeley *et al.* 2011). Climate change should variably impact tree species through growth (Ouédraogo *et al.* 2013; Wagner *et al.* 2014), recruitment (Clark *et al.* 2011) and mortality (Allen *et al.* 2010; Anderegg, Kane & Anderegg 2013) with consequences on tree species' relative abundances in the community. Tree species are characterized by functional traits (Violle *et al.* 2007) such as wood density (Chave *et al.* 2009; Vieilledent *et al.* 2012) and tree stature which includes tree maximal height and maximal diameter (King, Davies & Noor 2006; Poorter, Bongers & Bongers 2006; Barthelemy & Caraglio 2007). Because these traits determine tree and forest biomass (Baker *et al.* 2004; Vieilledent *et al.* 2012; Chave *et al.* 2014), the predicted shift in species range (Hannah *et al.* 2008) and species relative abundance (Feeley *et al.* 2011) with climate change should significantly impact forest carbon storage. Interestingly, in a study simulating potential tree species extinction scenarios in a Panamanian tropical forest, Bunker *et al.* (2005) underlined the fact that future carbon storage in tropical forests will be influenced strongly by future tree species composition. In their study, they simulated 18 possible extinction scenarios and showed that the loss of large-statured tree species (replaced by smaller-statured tree species) in a Panamanian forest would lead to a 29% decrease in the total forest carbon stock.

Although it is common to predict future species range using bioclimatic envelope models and climatic projections (Guisan & Zimmermann 2000; Pearson & Dawson 2003; Thuiller *et al.* 2005; Vieilledent *et al.* 2013a), it is difficult to predict changes in tree species composition and forest structure (tree height and diameter distribution), and thus forest carbon stocks, following climate change. Nonetheless, it is still possible to directly correlate forest biomass to climate. Recent empirical studies in tropical forests have shown the importance of climatic variables in determining tree stature and biomass (Feldpausch *et al.* 2011; Banin *et al.* 2012; Vieilledent *et al.* 2012; Chave *et al.* 2014) having consequences on carbon stocks at the forest stand level (Feldpausch *et al.* 2012). In particular, in a global study where 4004 trees from 58 tropical forest sites were harvested and measured, Chave *et al.* (2014) found that asymptotic tree height decreased with bioclimatic stress, that is with temperature and precipitation variability and drought intensity. Similarly, using a theoretical model based on scaling laws and energy budgets constrained by local resource limitations, Kempes *et al.* (2011) have demonstrated that maximal tree height increased with precipitation and decreased with temperature. Additional studies have shown that tree maximal size was highly correlated to forest biomass locally (Stegen *et al.* 2011; Michaletz *et al.* 2014). As a consequence, the climate should also have an effect at the ecosystem scale for determining forest carbon stocks. Only a few studies have investigated the link between climate and forest carbon stocks at the ecosystem scale using empirical correlative approaches (Keith, Mackey & Lindenmayer 2009; Stegen *et al.* 2011). Mixing data from boreal, temperate and tropical forests, the two studies by Keith, Mackey & Lindenmayer (2009) and Stegen *et al.* (2011) suggested that the role of climate was not consistent across forest types. As a result, they made no general predictions concerning changes in forest carbon stocks in response to changes in climate. Moreover, correlative models used to derive forest carbon maps at the global scale (Saatchi *et al.* 2011; Baccini *et al.* 2012) do not include explicative climatic variables and therefore cannot be used to predict future tropical forest carbon stocks under the effects of climate change.

In this study, we present the first attempt to project the effects of climate change on tropical forest carbon storage using correlative bioclimatic envelope models. To do so, we used a very large number of forest plots (1771) dispersed across Madagascar. Madagascar has a wide variety of climates and forest types and is thus particularly interesting for the study of the relationship between climate and tropical forest carbon stocks. The large climatic gradient on the island is associated with elevation and position relative to the dominant south-eastern winds (Goodman & Benstead 2003; Tadross *et al.* 2008) and contributes to define a large range of tropical forest types, from spiny dry forests in the subdesert Southern regions to cloud forests which are found at the top of the northern and eastern mountains. Using this large data set, we first modelled the relationship between climate and forest carbon storage and tested for a correlation between the two. We then used this correlative model to project the future national forest carbon stock under climate change and quantify the effect of climate change on the forest carbon storage. Lastly, we compared the effect of climate change to the effect of anthropogenic tropical deforestation in terms of carbon emissions and discuss the generalization of our results to other tropical regions.

Materials and methods

COMPILING FOREST INVENTORY DATA

We assembled data from nine forest inventories carried out over the period 1996–2013 [Table 1 and Vieilledent *et al.* (2016)]. Collaboration with different institutions (governmental institutions, conservation NGOs, research institutes) allowed us to obtain a large number of forest plots (1771) in the three forest ecoregions of Madagascar (moist, dry and spiny forest ecoregions, see Fig. 1). Ecoregions were defined on the basis of climatic and vegetation criteria using the climate classification by Cornet (1974) and the vegetation classification from the 1996 IEFN national forest inventory (Ministère de l'Environnement, 1996). For each of the forest plots, tree diameter was measured at 1·30 m (D in cm) using a metre tape and identified to the genus from vernacular names. Several trees were also measured in height (H in m) using either a clinometer (coupled to a transect tape to measure distance to tree) or an ultrasonic Vertex hypsometer. For all inventories with the exception of the IEFN inventory, all trees over 5 cm D were measured in concentric circular plots of variable radius depending on tree size. The largest radius was 30 m in moist forest (plot size of 0.28 ha) and 20 m in dry or spiny forest (plot size of 0.13 ha). The IEFN inventory (the largest inventory in the data set, providing 768 plots) used concentric circular plots for trees with $5 \leq D < 15$ cm but angle count plots (Bitterlich plots) for trees with $D \geq 15$ cm, with a basal area factor of 9 and 4 $\text{m}^2\ \text{ha}^{-1}$ for moist and spiny/dry forest, respectively.

COMPUTING TREE BIOMASS WITH PANTROPICAL ALLOMETRIC MODELS

We computed the above-ground biomass (AGB_i, in Mg) of each tree i using the pantropical biomass allometric equation developed by Chave *et al.* (2014): $AGB_i = 0.0673 \times (\rho_i D_i^2 H_i)^{0.976}$, ρ_i being the tree wood density (in g cm^{-3}). When tree height was not available, we used height–diameter allometric models based on tree height and diameter measurements from the forest inventories and one destructive study (Vieilledent *et al.* 2012). We used a power relationship between H and D: $\log(H_i) = \beta_0 + \beta_1 \log(D_i) + \varepsilon_i$, $\varepsilon_i \sim \text{Normal}(0,\sigma^2)$, and we fitted the model independently for the three forest types. We obtained three significantly different height–diameter allometric models, representative of the climatic and soil conditions of each ecoregion (Fig. S1). For a given diameter, trees are on average higher in the moist forest than in the dry and spiny forests. When assigning wood density to each tree, we used the following rules: (i) if the tree genus was present in one of the Malagasy wood-density data bases

Table 1. Forest inventories used in the analysis. We combined nine forest plot inventories with above-ground carbon density data. Data were collected between year 1996 and 2013 in the three types of forest in Madagascar (moist, dry and spiny forest). Eight institutions have collaborated to provide a total of 1771 plots spread over all Madagascar

Id	Name	Date	Ecoregion	Plot nb.	Institution
1	IEFN	1996	moist, dry and spiny	768	DGF
2	JariAla	2007	moist and dry	439	DGF/USAID
3	PHCF	2010	moist and spiny	92	Goodplanet/ WWF
4	CAZ-COFAV	2009	moist	117	CI
5	Makira	2010	moist	130	WCS
6	CI-forêt sèche	2011	dry	126	CI
7	Ranobe-PK32	2012	dry and spiny	14	WWF/Cirad
8	Kirindy	2012	dry	15	ONE/DGF
9	Itasy	2013	moist	70	ONE/DGF
	Total			1771	

(Rakotovao *et al.* 2011; Vieilledent *et al.* 2012), we computed the mean wood density at the genus level from these sources, (ii) if the tree genus was not present in the Malagasy data bases, we computed the mean wood density at the genus level from the global wood density data base (Chave *et al.* 2009), and (iii) if the tree genus was not present in the Malagasy or global wood density data bases or was undetermined (this was the case for 32% of the trees), we computed the mean wood density at the plot level using wood density values of all the trees in the plot whose genus was present in the data bases. Taking into account tree size and forest plot structure (radius for circular plots and basal area factor for Bitterlich plots), we converted each tree biomass AGB_i to a value of AGB per hectare. We summed these values for all trees ≥5 cm DBH at the plot level and obtained the $AGB_{\geq 5,j}$ (in Mg ha^{-1}) for each forest plot *j*. We obtained the above-ground carbon density $ACD_{\geq 5,j}$ (in Mg ha^{-1}) for each plot *j* assuming a carbon ratio of 0·47: $ACD_{\geq 5,j} = 0{\cdot}47\times AGB_{\geq 5,j}$.

SPATIAL ACD MODELLING FROM VEGETATION INDEXES, TOPOGRAPHY AND CLIMATE USING THE RANDOM FORESTS ALGORITHM

We modelled ACD spatially using three types of explicative variables: vegetation indices, topography and climatic variables. Vegetation indices were obtained from 250 m resolution MODIS (Moderate Resolution Imaging Spectroradiometer) satellite images from the years 2000 to 2010. We also utilized the annual vegetation continuous field per cent tree cover (VCF in %) available from the global land cover facility (DiMiceli *et al.* 2011). The per cent tree cover describes the percentage of a pixel which is covered by tree canopy. Lastly, we computed the mean annual enhanced vegetation index (EVI, from 0 to 1) from 16-day MODIS MOD13Q1 data (NASA-LP DAAC, 2014). Compared to the standard Normalized Difference Vegetation Index (NDVI), which is chlorophyll sensitive, the EVI is more responsive to canopy structural variations, including leaf area index, canopy type, plant physiognomy and canopy architecture. Moreover, EVI has an improved sensitivity in high biomass regions. Because forest plot inventory data were collected on different dates (from 1996 to 2013), we associated the measured $ACD_{\geq 5,j}$ for plot *j* with the mean of the three annual values of EVI and VCF at the closest years, denoted EVI_j and VCF_j. For examples, for plots sampled before 2002, we computed the mean EVI and VCF of years 2000, 2001 and 2002. For plots measured after 2008, we computed the mean EVI and VCF of years 2008, 2009 and 2010. For plots measured at years *y* between 2002 and 2008, we computed the mean EVI and VCF of years $y-1$, *y* and $y+1$. Using average values of EVI and VCF, we reduced the temporal noise associated with the year-to-year and seasonal variability of these indices. For the topography, we only used the elevation (E_j, in m) which was extracted from the 90 m resolution SRTM (Shuttle Radar Topography Mission) global elevation data set. Current (1950–2000) climatic data at 30 s (~1 km) resolution were obtained from the MadaClim website (http://madaclim.org) which provides WorldClim current climate data (Hijmans *et al.* 2005) specifically for Madagascar. For each plot *j*, we extracted the annual precipitation (P_j, in mm), the mean annual temperature (T_j, in °C) and the temperature seasonality (S_j, standard deviation of monthly temperature ×100).

We used the Random Forests algorithm to model ACD_j as a function of the vegetation, the elevation and the climate: $ACD_{\geq 5,j} = f\ (VCF_j, EVI_j, E_j, P_j, T_j, S_j)$. Random Forests is an ensemble learning method based on decision trees (Breiman 2001). Because it uses a nonparametric approach, Random Forests accommodates strong nonlinear relationships between the explicative variables and the response variable. Random Forests has been successfully used in previous scientific studies that modelled forest carbon stocks (Baccini *et al.* 2012; Mascaro *et al.* 2014). For our study, we performed the statistical analysis using the randomForest package (Liaw & Wiener 2002) available with the R software (R Development Core Team, 2014).

EVALUATING MODEL PERFORMANCE AND VARIABLE IMPORTANCE

To evaluate model performance, we repeated a cross-validation procedure ten times. About 70% of the data were selected at random to be used as training data to fit the model. The remaining 30% was used as test data to compute several model performance indices. First, we computed the coefficient of determination (R^2, in %) which indicates the part of the observed ACD variability explained by the model. Secondly, we computed the root-mean-square error (RMSE, in Mg ha^{-1}) which measures the average difference between values predicted by the model and observations. Thirdly, we computed the mean bias (*B*, in %) indicating an average over- or underestimation of ACD values by the model. We computed the mean and standard deviation of the ten values obtained for the performance indices through the repeated cross-validation procedure. We also investigated the relative importance of each variable in determining ACD by computing the percentage increase in the mean standard error when the variable was randomly permuted (%IncMSE) and observing the graphical relationship between variables and ACD using partial dependence plots (see randomForest package manual for details).

DERIVING A 2010 FOREST CARBON MAP

We resampled the explicative variables data at 250 m resolution and used EVI and VCF from 2010 to derive a national carbon map at 250 m resolution from our ACD model. Because our data set included values of ACD observed only in forest habitat (and not in cropland or savanna for example), we made the assumption that our carbon map was not valid in non-forested regions. We thus masked the carbon map with a map depicting Madagascar's forest in 2010. This forest map was derived from the 30 m resolution 2000 forest map by Harper

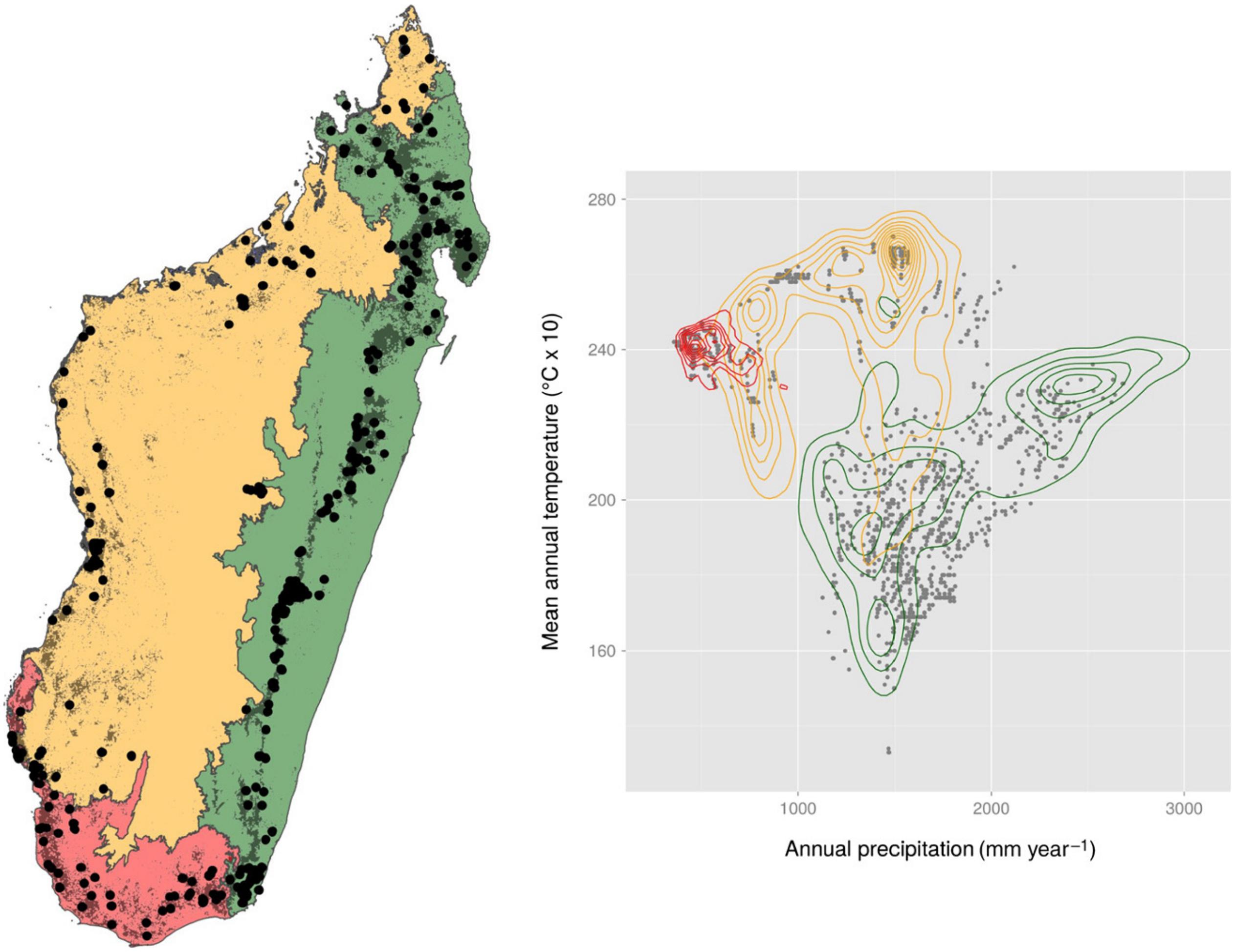

Fig. 1. Climatic ecoregions and location of forest plots. Left panel: Madagascar can be divided into three climatic ecoregions with three forest types: the moist forest in the East (green), the dry forest in the West (orange) and the spiny forest in the South (red). Ecoregions were defined following climatic (Cornet 1974) and vegetation (Ministère de l'Environnement, 1996) criteria. The 1771 forest plots of our study (black points) cover as much as possible the remaining tropical forest in 2010 (dark grey areas). Right panel: climate in the three forest types of Madagascar can be represented by 2D densities (coloured curves) obtained from sampling at random twenty thousand points in each forest type. The three forest types are characterized by significantly different climatic conditions and a large gradient of precipitation and temperature is observed. The 1771 forest plots of our study (dark grey points) are representative of the climatic conditions found in Madagascar forests.

et al. (2007). On Harper's map, ~200 000 ha clouds are present over the ~4.2 million ha moist forest ecoregion (4.8% of clouds). To remove these clouds, we used the 2000 cloud-free tree per cent cover map provided by Hansen *et al.* (2013) (also at 30 m resolution) and we chose a threshold of 75% of tree cover to decide whether to replace cloud pixels with forest or non-forest pixels (Achard *et al.* 2014). We thus obtained a cloud-free year 2000 forest map for Madagascar. From this map, using deforestation data from 2000 to 2010 by Hansen *et al.* (2013), we obtained a cloud-free forest map in 2010 at 30 m resolution. We resampled this forest map to 250 m resolution using the nearest-neighbour method. Combining the carbon map and the forest map, we obtained a forest carbon map in 2010 for Madagascar at 250 m resolution. We compared the predictions of our carbon map at 250 m resolution with the measured ACD data from the 1771 forest inventories and computed the resulting R^2 and RMSE.

COMPARISONS WITH GLOBAL CARBON MAPS

We tested whether our 2010 forest carbon map for Madagascar at 250 m was more accurate than the two global carbon maps provided by Saatchi *et al.* (2011) and Baccini *et al.* (2012). Saatchi's map is at 1 km resolution and Baccini's map is at 500 m resolution. To allow a fair comparison between the predictions of the three maps at different resolutions, we resampled the three maps to 1 km resolution using a bilinear interpolation. We compared the predictions of the three maps with the measured ACD data, and we computed the resulting R^2 and RMSE. At the regional scale, we also compared the mean and standard deviation of the predicted ACD values by forest type using our map at 250 m, Saatchi's map at 1 km and Baccini's map at 500 m. We also compared the values of total forest carbon stock at the national scale using the three maps.

FORECASTING THE EFFECTS OF CLIMATE CHANGE ON FOREST CARBON STORAGE

We used the correlative bioclimatic envelop model we fitted previously (see Section 'Spatial ACD modelling from vegetation indexes, topography and climate using the Random Forests algorithm') to predict the potential future forest carbon stocks at 250 m for Madagascar in 2050 and 2080 considering climate change. Because changes due to climatic variables were our key focus, we assumed no land-use change (no deforestation) between 2010 and 2080. Also, we assumed no change in the values of the vegetation indices in the future. As a consequence, our predictions only indicate the marginal effect of the climatic change on forest carbon stocks through changes in the values of the climatic variables.

For future climatic data in 2050 and 2080, we used the projections of seven global climate models (GCMs), following the representative concentration pathways (RCPs) 4.5 and 8.5. GCMs were obtained from the Coupled Model Intercomparison Project Phase 5 (CMIP5) of the Intergovernmental Panel on Climate Change (IPCC). We used the following seven GCMs: ACCESS 1.0, CCSM4, GISS-E2-R, HadGEM2-ES, IPSL-CM5ALR, MIROC5 and NorESM1-M. Climatic data were obtained from the MadaClim website (http://madaclim.org) which provides the CCAFS GCM future climate data (http://www.ccafs-climate.org/data/) specifically for Madagascar. We then compared these changes in forest carbon stock induced by climate change to carbon emissions that would be associated with a spatially homogeneous deforestation rate of 0.5% y^{-1}. This value corresponds to the last estimate (period 2000–2010) of the national deforestation rate for Madagascar (Hansen *et al.* 2013; ONE *et al.*, 2013).

Results

SPATIAL DISTRIBUTION OF FOREST CARBON STOCKS IN MADAGASCAR

We obtained very coherent spatial patterns of forest carbon stocks at the national scale for Madagascar. In particular, we were able to clearly differentiate the carbon stocks for the spiny, dry and moist forests (Fig. 2) for which we obtained mean carbon stocks of 17 (±6), 52 (±25) and 150 (±33) Mg ha^{-1}, respectively (Table 2). The highest carbon stocks for Madagascar (> 200 Mg ha^{-1}) were found in the Makira and Masoala peninsula forests around the Antongila bay in north-east Madagascar (Fig. 2). These hilly forests are known to form the largest tracts of intact moist forest remaining in Madagascar. For the 250 m map (with spatial grid cells of 6.25 ha), the maximal predicted value of the forest carbon stock was 261 Mg ha^{-1}, which is realistic for Madagascar forests at this resolution. In comparison, the maximal carbon stock measured on much smaller forest plots (< 0.3 ha) was of 348 Mg ha^{-1}. Moreover, the effect of climatic and altitudinal gradients on the forest carbon stocks was clearly visible on the forest carbon map (Fig. 2). In particular, we were able to observe a rapid drop of the forest carbon stock in the extreme south of Madagascar which corresponds to the rapid transition from the eastern moist forest receiving high precipitation to the southern xeric spiny forest in the mountains' rain shadow (Fig. 2).

Also, we were able to find much higher carbon stocks in the Amber Mountain (850 to 1475 m of altitude) at the extreme north of Madagascar, where forests benefit of a microclimate with high precipitation in the middle of the dry ecoregion.

MODEL PERFORMANCE AND VARIABLE IMPORTANCE

The cross-validation results indicated that the model had good predictive abilities with a relatively high coefficient of determination ($R^2 = 64(\pm 2)\%$), and relatively low root-mean-square error and bias [RMSE = 44(±2) Mg ha^{-1} and $B = +31(\pm 4)\%$]. In terms of explicative importance, variables were classified in the following decreasing order: temperature seasonality (*S*, 68% of increase in the mean square error when the variable was randomly permuted), precipitation (*P*, 49%), mean annual temperature (*T*, 48%), elevation (45%), *EVI* (40%) and *VCF* (38%). All variables were highly explicative of the amount of forest carbon stock, but climatic variables (temperature seasonality, annual precipitations and mean annual temperature) were found to be the most important, relative to elevation and vegetation indices. Analysing the relationship between explicative variables and ACD, we observed biologically coherent patterns (Fig. 3). ACD was higher at intermediate elevation (500–1200 m) and increased almost linearly with EVI and VCF. Regarding climatic variables,

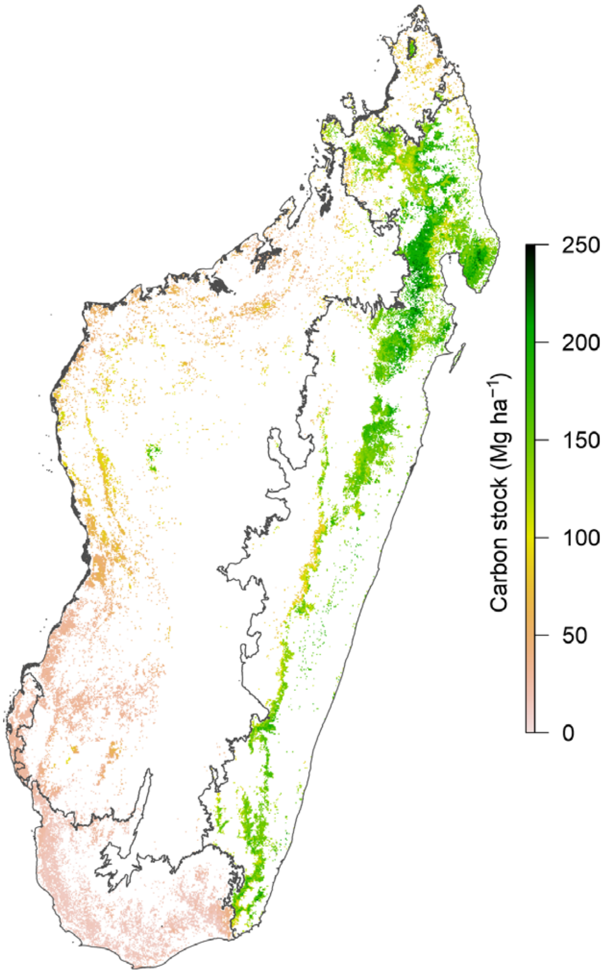

Fig. 2. Relationships between explicative variables and ACD. Graphics shows the marginal effect of the variable on ACD. Range of predicted ACD is reduced compared to the observed range of ACD in forest plots because variables other than the target variable are set to their mean values. Hash marks at the bottom of the plot indicate the deciles of the explicative variable. Percentage in the top-left or top-right corner of each panel is the percentage of increase in mean square error when the variable was randomly permuted, which indicates the variable relative importance in determining ACD.

Table 2. Comparing observed and predicted mean ACD (Mg ha^{-1}) by forest type with global carbon maps. Forest areas in 2010 are in thousands of ha and mean carbon stocks are in Mg ha^{-1}. Numbers in parentheses represent the standard deviations. Column 'Mean obs.' gives observed mean carbon stocks from forest plot inventories and column 'Mean 250 m' gives predicted mean carbon stocks from the national forest carbon map at 250 m. While global carbon maps gave relatively good estimates of the mean carbon stocks for the moist forest in Madagascar, they failed at providing good estimates and differentiating clearly the carbon stocks in the dry and spiny forests

Ecoregion	Forest area	Plot nb.	Mean obs.	Mean 250 m	Saatchi 1 km	Baccini 500 m
Moist	4625	1190	136 (67)	150 (33)	128 (53)	113 (36)
Dry	2725	367	51 (33)	52 (25)	41 (21)	33 (20)
Spiny	1741	214	18 (11)	17 (6)	34 (19)	22 (9)

ACD decreased dramatically with increasingly stressful climatic conditions. We identified the climatic tipping points beyond which the ACD dropped: for $T > 21$°C, $S > 2100$ and $P < 1100$ mm y^{-1} (Fig. 3).

COMPARISON WITH GLOBAL CARBON MAPS

At 1 km resolution, our map provided much more accurate predictions of ACD values (R^2 = 0.64, RMSE = 44 Mg ha^{-1}) than Saatchi's or Baccini's maps (R^2 = 0.26, RMSE = 64 Mg ha^{-1} and R^2 = 0.17, RMSE = 63 Mg ha^{-1}, respectively). The best predictions were obtained using our model at 250 m resolution (R^2 = 0.70, RMSE = 40 Mg ha^{-1}) (Fig. S2). At the forest type level (Table 2), the global carbon maps gave relatively good estimates of the mean carbon stocks for the moist forest in Madagascar, but conversely, they failed to provide good estimates and differentiate clearly between the dry and spiny forests in terms of carbon stocks. Using our map at 250 m (Fig. 2), we estimated Madagascar's total forest carbon stock to be 873086 Gg (1Gg = 10^9 g) in 2010. Computing the total forest carbon stock using mean ACD estimates by forest type from Saatchi's and Baccini's maps (Table 2) led to lower estimations of the total carbon stock for Madagascar *c.* 2010 (764168 (−12%) and 652896 (−25%) Gg, respectively).

POTENTIAL IMPACT OF CLIMATE CHANGE ON CARBON EMISSIONS

Comparing the current climate in Madagascar with the projected climate in 2080 following RCP 8.5, temperature seasonality and mean annual temperature are predicted to increase (of +138 SD × 100 and +3.7°C on average, respectively), while precipitation is predicted to decrease (of −107 mm y^{-1} on average) over almost the entire forest area (Fig. S3). Using climatic projections following the RCP 8.5 and our forest carbon stock model, we forecasted the changes in forest carbon stocks by the year 2080 (Fig. 4). Most of Madagascar forests are likely to experience a decrease of their carbon stock, up to −150 Mg ha^{-1} on the period 2010–2080 for the Madagascar moist forest. In some areas, in particular in the spiny forest, a limited increase of the carbon stock is expected (< 50 Mg ha^{-1}). The increase of the forest carbon stock is associated with the predicted future increase of the precipitation in these areas (Fig. S3). At the national scale, these changes should lead to an average forest carbon stock loss of 17% (range: 7–24%) by the year 2080 (Fig. 4 and Table S1). Following RCP 4·5, the forest carbon stock loss ranged from 2 to 13% (Table S1). Following RCP 8·5, the total forest carbon stock would drop progressively from 873086 Gg in 2010, to 799 097 Gg (−8%) in 2050 and 720944 Gg (−17%) in 2080 (Fig. 4). For a comparison, a spatially homogeneous deforestation of 0·5% y^{-1} from 2010 to 2080 over Madagascar would lead to a residual carbon stock of 614714 Gg (−30%).

Discussion

AN ACCURATE FOREST CARBON MAP FOR MADAGASCAR

Using a large data set including 1771 forest plots spread across the entire country and representative of the three tropical forest types existing in Madagascar, we were able to fit a good predictive model (R^2 = 64%, RMSE = 44 Mg ha^{-1} and B = +31%). We obtained an accurate (R^2 = 0.70, RMSE = 40 Mg ha^{-1}) national forest carbon map at 250 m resolution for Madagascar for year 2010. In a study mapping forest carbon on 16 million hectares in the Western Amazon and using a more sophisticated model with spatial autocorrelation, Mascaro *et al.* (2014) obtained a map with a lower R^2 (R^2 = 59%) but a smaller RMSE (RMSE = 26 Mg ha^{-1}). In their case, the initial variability of observed ACD was limited as they used 1 km LiDAR-based estimates (and not estimates at a point), thus potentially reducing the residual values between predicted and observed ACD. Regarding forest carbon maps that can be used at the national scale for Madagascar, the two global maps by Saatchi *et al.* (2011) and Baccini *et al.* (2012) have a coarser resolution (500 m and 1 km resolution). We showed that these two global maps were less accurate than the map we obtained at 250 m resolution ($R^2 \leq 26$ and RMSE ≥ 63 Mg ha^{-1}) and that they failed to differentiate clearly between the carbon stocks in the spiny and dry forests of Madagascar. When used at the national level, the two global maps underestimated (by more than 12%) the total carbon stock of Madagascar, in comparison with the map produced herein. The lower accuracy of the global carbon maps can be explained by two factors. First, only Saatchi's map (which is the most accurate of the two maps according to our study) utilized forest plot data from

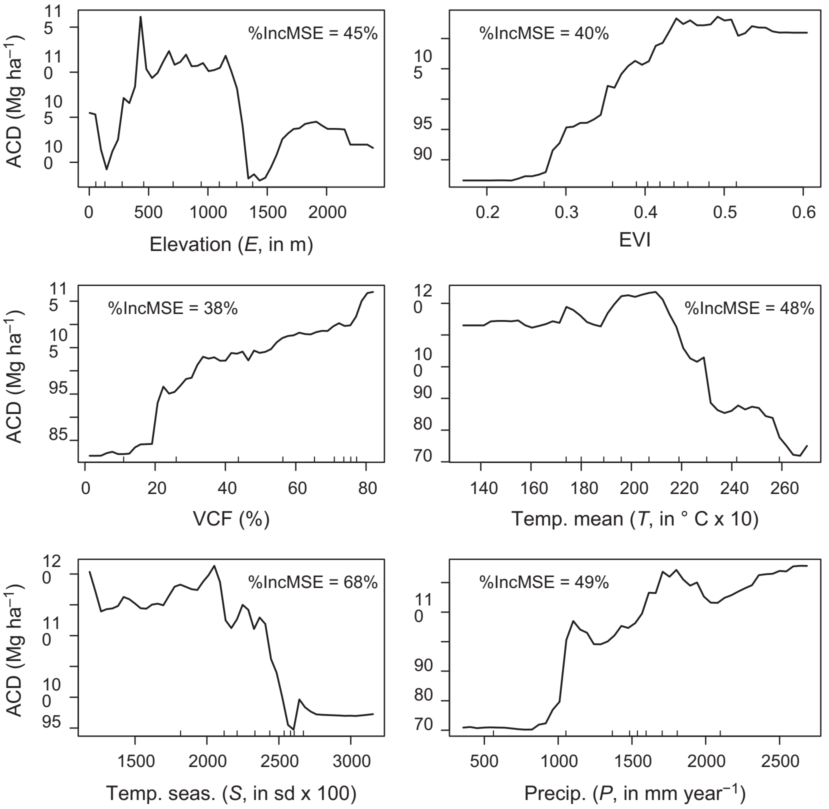

Fig. 3. Forest carbon map in 2010 for Madagascar. We derived a national forest carbon map in 2010 for Madagascar at 250 m resolution. We fitted our model using above-ground carbon density for 1771 forest plots measured between 1996 and 2013. Our model included six explicative variables: two vegetation indexes (VCF and EVI from 2000-2010 MODIS satellite images at 250 m), one topographic variable (elevation from SRTM at 90 m) and three climatic variables [mean annual temperature, mean annual precipitation and temperature seasonality from WorldClim at 30 arc-seconds (~1 km)]. Our predictions are limited to the extent of the forest in 2010. Clear differences appear for the forest carbon stocks between the three ecoregions including moist, dry and spiny forest (see black lines for delimitations).

Madagascar (202 plots) to calibrate the statistical models used to predict ACD. Regarding the lack of distinction between spiny and dry forest carbon stocks, the plots used to calibrate Saatchi's model were located in the moist forest and were thus not representative of Madagascar's other forest types. The fact that a substantial number of carefully established field plots are necessary to derive accurate ACD maps has been previously underlined by Mitchard *et al.* (2014). Secondly, neither Baccini's nor Saatchi's maps included climatic variables as explicative factors of ACD, while we have shown in our study that they were more important explicative variables than the altitude and the vegetation indices.

EFFECTS OF CLIMATE ON FOREST CARBON STOCKS

The tree height is a key variable determining tree biomass (Vieilledent *et al.* 2012; Chave *et al.* 2014). Recent empirical and theoretical studies have emphasized the importance of climatic variables in determining the tree height–diameter relationship (Banin *et al.* 2012; Chave *et al.* 2014; Feldpausch *et al.* 2011) and the tree maximal height (Kempes *et al.* 2011). In a pantropical study, Chave *et al.* (2014) have demonstrated that tree height decreased with increasing temperature seasonality, precipitation seasonality and climatic water deficit. Chave *et al.* (2014) have shown that temperature seasonality (a proxy for the length of the growing season) was by far the most important climatic variable in explaining the tree height–diameter relationship and consequently tree biomass. In our study, we also identified temperature seasonality as being the most important variable determining forest biomass at the plot level (with a decrease of ACD with temperature seasonality), thus confirming the results obtained by Chave *et al.* (2014). In a theoretical study, based on scaling laws and energy budgets constrained by local resource limitations, Kempes *et al.* (2011) have demonstrated that maximal tree height increased with precipitation and decreased with temperature, thus corroborating the results of our study.

At the forest ecosystem level, Fischer *et al.* (2014) found a pattern similar to ours regarding the relationship between forest carbon stock and precipitation in the moist forests of Madagascar. The authors identified a tipping point around 2000 mm yr^{-1} for precipitation under which the forest carbon stock was rapidly decreasing. While they argued that a temporary 20% reduced rainfall would have a moderate impact on the forest carbon stock (due to the soil water content that would support tree growth), they found that a decrease of 50% of rainfall would lower the carbon stocks by about 20%. In a large-scale study using data from 271 plots from temperate and tropical forests in North, Central and South America, Stegen *et al.* (2011) found weak relationships between forest biomass and climate. No significant relationships was found between forest biomass and mean annual temperature across forest types and a weak, albeit significant, positive relationship was found between forest biomass and annual precipitation. In another study using biomass data from 136 plots from the world's most carbon-dense primary forests, Keith, Mackey & Lindenmayer (2009) concluded that the highest biomass carbon density occurs in cool, moderately wet climates in temperate moist forest biomes. However, Fig. 3 in

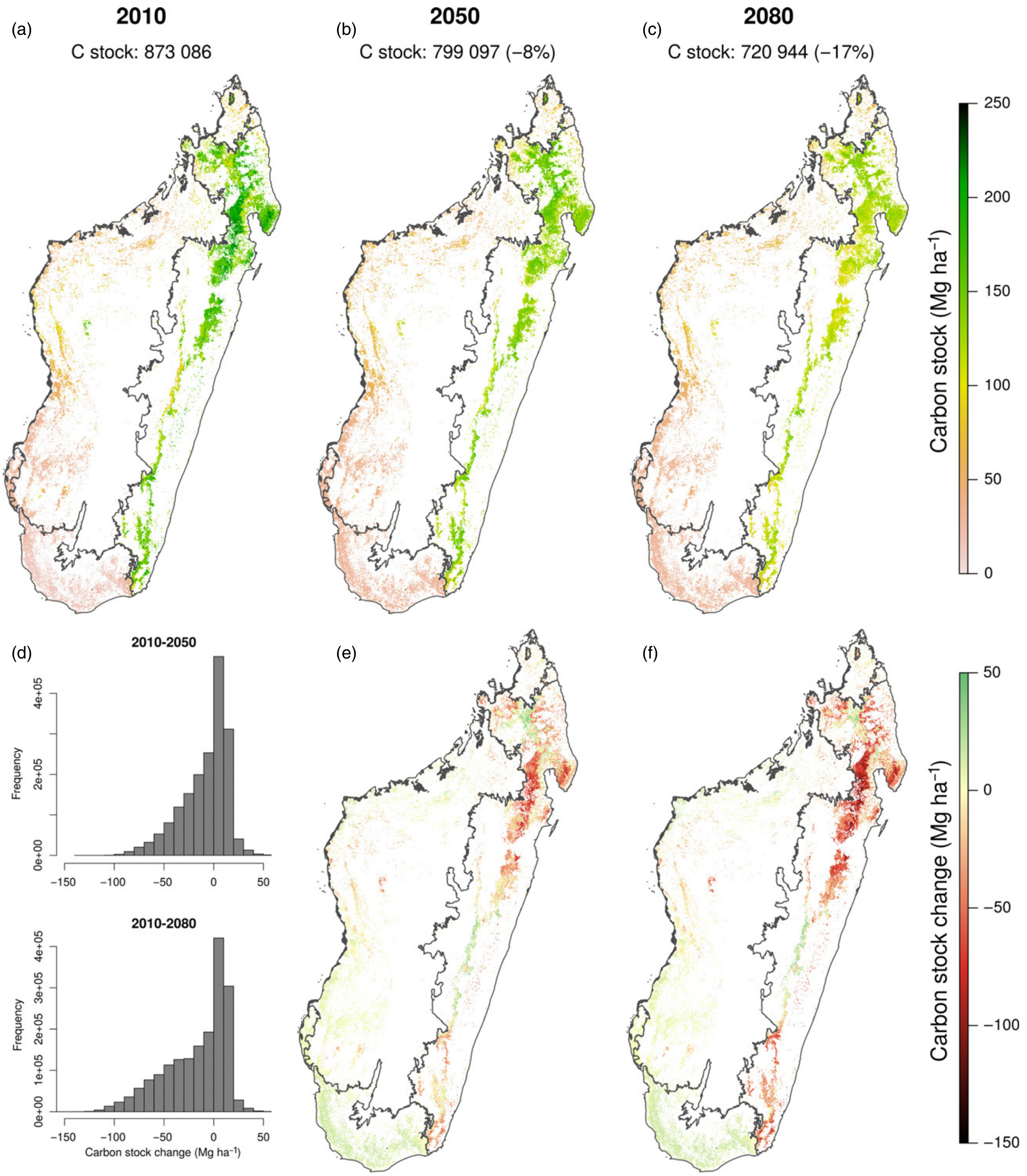

Fig. 4. Forest carbon stock evolution with climate change in Madagascar. (a–c): Maps of Madagascar forest carbon stocks for the years 2010, 2050 and 2080. Using climate projections in 2050 and 2080 (from seven IPCC CMIP5 global climate models following the RCP 8.5) and our carbon stock model, we estimated the average forest carbon stock in 2050 and 2080 for Madagascar. At the national scale, climate change would result in a progressive decrease of the total forest carbon stock (see C stocks, in Gg = 10^9 g) of −9% and −17% for years 2050 and 2080, respectively. (d): Distributions of the 250 m resolution forest pixels as a function of the carbon stock change for the periods 2010–2050 and 2010–2080. (e–f): Carbon stock change on the periods 2010–2050 and 2010–2080. Moist forest in the East should experience the greatest changes with a drastic decrease of the forest carbon stock.

Keith, Mackey & Lindenmayer (2009) and Fig. 4 in Stegen *et al.* (2011) show that for sites with a tropical climate (excluding boreal and temperate sites with mean annual temperature < 15°C), forests under warmer and drier climates (with higher mean annual temperature and lower annual precipitation) appear to have lower carbon stocks. Results obtained by Keith, Mackey & Lindenmayer (2009) and Stegen *et al.* (2011) are then in line with the results obtained by Chave *et al.* (2014) regarding the relationship between tree biomass and climate in tropical forests and are also comparable with the results of our study. More work is still required in order to understand more precisely the effect of climate on forest carbon storage across other forest types such as boreal and temperate forests (Keith, Mackey & Lindenmayer 2009; Stegen *et al.* 2011; Koven 2013). One difficulty is that temperate regions have a diversity of forest types that support a wide range of mature carbon stocks or have a long land-use history with reduced carbon stocks. As a consequence, past studies comparing carbon stocks in tropical and temperate forests have led to contrasting conclusions. For example, Houghton (2005) and Saatchi *et al.* (2011) have shown that tropical forests have a much higher mean biomass (*c.* 130 Mg ha^{-1}) than temperate forests (*c.* 50 Mg ha^{-1}), which contradicts the results reported by Keith, Mackey & Lindenmayer (2009).

The results of our study at the forest ecosystem scale, together with the previous results obtained by Chave *et al.* (2014) at the tree level, are coherent with the known physiological and ecological mechanisms explaining the relationship between forest biomass and climate. Several studies have shown that climate (mainly through growing season length and water availability) directly impacts tree species metabolic rates such as respiration and photosynthesis, having direct ($\sim$ daily or yearly) repercussions on tree species growth and forest net primary productivity (Huxman *et al.* 2004; Cox *et al.* 2013). On a larger time scale ($\sim$ decades), climate drives tree species demographic rates such as mortality (Allen *et al.* 2010; Anderegg, Kane & Anderegg 2013) and fecundity (Clark *et al.* 2011), thus determining tree species composition and forest structure (Feeley *et al.* 2011) which in turn define forest carbon stocks (Bunker *et al.* 2005). On this point, it is interesting to see that the estimate of 29% decrease in the forest carbon stock reported by Bunker *et al.* (2005), which is associated with a replacement of large-statured tree species with smaller-statured tree species, is close to our estimate of 7–24%. At larger geographical scales and on an even larger time scales ($\sim$ centuries), tree species composition is assumed to be the result of a selection pressure with an adaptation to local climates (Iverson & Prasad 1998; Clark & McLachnan 2003; Michaletz *et al.* 2014). Metabolic scaling theory (Michaletz *et al.* 2014) and recent empirical data (Stegen *et al.* 2011) led to the conclusion that forest biomass is strongly correlated to the size of the largest individual, which is in itself strongly dictated by tree species architectural characteristics (Poorter, Bongers & Bongers 2006; Barthelemy & Caraglio 2007) and the local climate (Feldpausch *et al.* 2011; Kempes *et al.* 2011; Banin *et al.* 2012; Vieilledent *et al.* 2012; Chave *et al.* 2014). In Madagascar, tree species composition and climatic conditions in the moist, dry and spiny forest are substantially different (Goodman & Benstead 2003; Harper *et al.* 2007) resulting in significantly different sizes for the largest individual between forest types (Fig. S1 and Vieilledent *et al.* (2012)) and in significantly different forest carbon stocks (Fig. 2). Significant changes in tree species distribution are expected in Madagascar (Hannah *et al.* 2008; Vieilledent, Grinand & Vaudry 2013b). Tree species adapted to drier conditions and to shorter growing seasons are likely to increase their relative abundance in forest communities locally (Feeley *et al.* 2011) or to expand their geographical range (Hannah *et al.* 2008). It has been demonstrated that these tree species are usually characterized by lower asymptotic heights (Vieilledent *et al.* 2012; Chave *et al.* 2014) and lower biomass. Climate change would thus indirectly induce a decrease of the forest carbon stock through the selection of small-statured tree species.

TROPICAL FORESTS AS A CARBON SINK: COMPARING DGVMS AND BIOCLIMATIC ENVELOPE MODEL OUTPUTS

Our model estimates that, in Madagascar, changes in climatic conditions predicted to occur between 2010 and 2080 will cause the loss of 17% (range: 7–24%) of the forest carbon stock and would result in the emissions of 152142 Gg of carbon into the atmosphere. Climate change induced emissions would be of the same order of magnitude as the emissions associated with projected anthropogenic deforestation on the same period of time, with a loss of 30% of the forest carbon stock and emissions of 258372 Gg of carbon into the atmosphere. At present, most DGVMs also simulate a decrease of the vegetation carbon stock in response to reduction in precipitation and increase in temperature (Sitch *et al.* 2008; Cox *et al.* 2013; Huntingford *et al.* 2013). For example, Huntingford *et al.* (2013) estimated a decrease from 5 to 30 Mg ha^{-1} of the vegetation carbon stock in tropical Africa between 1860 and 2100 under the effect of increasing temperature (Fig. SI2 in the cited paper). But the strong decrease of the vegetation carbon stock due to climate change would be largely compensated by the fertilization effect of CO_2 modelled in DGVMs. Accounting for both climate change and CO_2 fertilization, Huntingford *et al.* (2013) estimated an average increase of 30 Mg ha^{-1} (+18%) of the African tropical forest carbon stock between 1980 and 2100 under IPCC business-as-usual SRES A2 scenario. Thus, most actual DGVMs predict a resilience of tropical forests to climate change due to an increase of tree growth (Sitch *et al.* 2008; Cox *et al.* 2013; Huntingford *et al.* 2013). Compared to DGVMs, our model does not include the direct effect of CO_2 fertilization on forest growth and resulting forest carbon stock. Indeed, higher CO_2 concentration is expected to raise plant photosynthetic rates and enhance water-use efficiency (Bonan 2008). However, there is no empirical evidence that these physiological responses do increase carbon sequestration in natural tropical forests (van der Sleen *et al.* 2015). For example, CO_2 fertilization might lead to an increase of tree growth but also to an increase of tree mortality due to faster growth (Brienen *et al.* 2015). Moreover, some studies showed that productivity may eventually become constrained by nutrient limitation (Norby *et al.* 2010) or climate stress (Perry *et al.* 2013). Finally, CO_2 enrichment experiments showing the CO_2 fertilization effect have been conducted in temperate forests (Norby *et al.* 2010) but not yet in tropical forests (but see Tollefson (2013)). As a consequence, DGVMs might overestimate the sink capacity of tropical forests (van der Sleen *et al.* 2015). Although not taking into account the potential effect of CO_2 fertilization, our forest carbon model provides more insight about the vegetation response to changes in temperature and precipitation, which constitutes the largest source of variability in DGVM outputs (Sitch *et al.* 2008; Cox *et al.* 2013; Huntingford *et al.* 2013).

Our approach shares the same hypothesis as when bioclimatic envelope models are used to predict the effects of climate change on species distribution (Pearson & Dawson 2003). In particular, for the forecast of future forest carbon stocks, we assumed that tree species will be able to track climate change (full dispersal hypothesis). Also, we assumed no change in the values of the vegetation indices in the future whereas climate change should impact them. These two hypotheses are conservative regarding the main result of our study which predicts a decrease of the forest carbon stock in Madagascar with climate change. Given the velocity of climate change (Loarie *et al.* 2009) and the difficulties experienced by tree species to migrate and track climate change (Zhu, Woodall & Clark 2012), shifts in species distribution at large geographical scale are uncertain. More likely, tree species will experience range contraction (Zhu, Woodall & Clark 2012; Vieilledent, Grinand & Vaudry 2013b) and climate change could lead to widespread tree-mortality events (Anderegg, Kane & Anderegg 2013; Brienen *et al.* 2015). Also, it is unlikely that vegetation indices will increase with climate change. Constant or lower values of vegetation indices due to an increase in the abundance of small-statured tree individuals and species are expected. Considering these two hypotheses, it is likely that our model underestimates the loss of forest carbon stock that would be associated with climate change.

At the global scale, climate observations and model predictions suggest continued increases in temperature (Hulme & Viner 1998) and decreases in precipitation over much of the humid tropics (Malhi & Wright 2004) thus suggesting a potential decrease in tropical tree growth and height in the future. Regarding seasonality, changes in rainfall seasonality are expected throughout the tropics (Feng, Porporato & Rodriguez-Iturbe 2013), but more research is still needed to be able to interpret these seasonal changes in terms of potential impacts on tree species size and forest carbon storage. Considering our results and those from previous studies (Bunker *et al.* 2005; Chave *et al.* 2014; van der Sleen *et al.* 2015), a substantial part of the tropical forest carbon stock is likely to be released into the atmosphere under the effect of climate change. On this basis, the recent simulated resilience of tropical forests to climate change with DGVMs, which relies mostly on the strong CO_2 fertilization effect (Sitch *et al.* 2008; Cox *et al.* 2013; Huntingford *et al.* 2013) may be questioned. The decrease of tropical forest carbon stocks with climate change, leading to a carbon-cycle feedback, should not be neglected and might be of the same order of magnitude as tropical anthropogenic deforestation regarding CO_2 emissions in the atmosphere.

Acknowledgements

Financial support was provided by Cirad, AFD (Agence Française de Développement) through the AT-REDD+ Madagascar project and FRB–FFEM (Fondation pour la Recherche sur la Biodiversité – Fond Français pour l'Environnement Mondial) through the BioSceneMada project (project agreement AAP-SCEN-2013 I). We would also like to thank all the people who contributed to the forest inventories in the field. Lastly, this work would not have been possible without the willingness of governmental officials, conservation NGOs and research institutes in Madagascar to share their forest inventory data for the establishment of a national forest carbon map. We thank them for their support.

Data accessibility

The following data are accessible on the Dryad digital repository associated with this study (see Vieilledent *et al.* (2016) and http://dx.doi.org/10.5061/dryad.9ph68):

- Above-ground carbon density (ACD) data.
- Present and future climatic data for Madagascar.
- Additional explicative variables (elevation, EVI and VCF) used to derive the forest carbon map.
- R script that can be used to fully reproduce the results of the study.
- Random Forests model used to derive the forest carbon maps.
- Madagascar 2010 forest carbon map at 250 m resolution.

References

Achard, F., Beuchle, R., Mayaux, P., Stibig, H.J., Bodart, C., Brink, A. *et al.* (2014) Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Global Change Biology*, **20**, 2540–2554.

Adams, H.D., Williams, A.P., Xu, C., Rauscher, S.A., Jiang, X. & McDowell, N.G. (2013) Empirical and process-based approaches to climate-induced forest mortality models. *Frontiers in Plant Science*, **4**.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Anderegg, W.R., Kane, J.M. & Anderegg, L.D. (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, **3**, 30–36.

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. *et al.* (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.

Banin, L., Feldpausch, T.R., Phillips, O.L., Baker, T.R., Lloyd, J., Affum-Baffoe, K. *et al.* (2012) What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography*, **21**, 1179–1190.

Barthelemy, D. & Caraglio, Y. (2007) Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany*, **99**, 375–407.

Bonan, G.B. (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449.

Breiman, L. (2001) Random Forests. *Machine Learning*, **45**, 5–32.

Brienen, R., Phillips, O., Feldpausch, T., Gloor, E., Baker, T., Lloyd, J. *et al.* (2015) Long-term decline of the amazon carbon sink. *Nature*, **519**, 344–348.

Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M. & Naeem, S. (2005) Species loss and above-ground carbon storage in a tropical forest. *Science*, **310**, 1029–1031.

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., Réjou-Méchain, M., Burquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B. *et al.* (2014) Improved allometric models to estimate the above-ground biomass of tropical trees. *Global Change Biology*, **20**, 3177–3190.

Clark, J.S. & McLachnan, J.S. (2003) Stability of forest biodiversity. *Nature*, **423**, 635–638.

Clark, J.S., Bell, D.M., Hersh, M.H. & Nichols, L. (2011) Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology*, **17**, 1834–1849.

Cornet, A. (1974) *Essai de cartographie bioclimatique à Madagascar*. Tech. rep, Orstom, **15**, 1–13.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.

Cox, P.M., Pearson, D., Booth, B.B., Friedlingstein, P., Huntingford, C., Jones, C.D. & Luke, C.M. (2013) Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature*, **494**, 341–344.

Cramer, W., Bondeau, A., Schaphoff, S., Lucht, W., Smith, B. & Sitch, S. (2004) Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **359**, 331–343.

DiMiceli, C., Carroll, M., Sohlberg, R., Huang, C., Hansen, M. & Townshend, J. (2011) Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000–2010, collection 5 percent tree cover. University of Maryland, College Park, MD, USA.

Feeley, K.J., Davies, S.J., Perez, R., Hubbell, S.P. & Foster, R.B. (2011) Directional changes in the species composition of a tropical forest. *Ecology*, **92**, 871–882.

Feldpausch, T., Banin, L., Phillips, O., Baker, T., Lewis, S., Quesada, C., Affum-Baffoe, K., Arets, E., Berry, N. & Bird, M. (2011) Height-diameter allometry of tropical forest trees. *Biogeosciences*, **8**, 1081–1106.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, E., Monteagudo Mendoza, A. *et al.* (2012) Tree height integrated into pan-tropical forest biomass estimates. *Biogeosciences*, **9**, 2567–2622.

Feng, X., Porporato, A. & Rodriguez-Iturbe, I. (2013) Changes in rainfall seasonality in the tropics. *Nature Climate Change*, **3**, 811–815.

Fischer, R., Armstrong, A., Shugart, H.H. & Huth, A. (2014) Simulating the impacts of reduced rainfall on carbon stocks and net ecosystem exchange in a tropical forest. *Environmental Modelling & Software*, **52**, 200–206.

Goodman, S. & Benstead, J. (2003) *The natural history of Madagascar*, p. 1709. University of Chicago Press, Chicago, IL, USA.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Hannah, L., Dave, R., Lowry, P.P., Andelman, S., Andrianarisata, M., Andriamaro, L. *et al.* (2008) Climate change adaptation for conservation in Madagascar. *Biology Letters*, **4**, 590–594.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A. *et al.* (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**, 850–853.

Harper, G.J., Steininger, M.K., Tucker, C.J., Juhn, D. & Hawkins, F. (2007) Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, **34**, 325–333.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Houghton, R. (2005) Above-Ground forest biomass and the global carbon balance. *Global Change Biology*, **11**, 945–958.

Hulme, M. & Viner, D. (1998) A climate change scenario for the tropics. *Potential Impacts of Climate Change on Tropical Forest Ecosystems* (ed. A. Markham) pp. 5–36. Springer, Dordrecht, The Netherlands.

Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L.M., Sitch, S., Fisher, R. *et al.* (2013) Simulated resilience of tropical rainforests to CO_2-induced climate change. *Nature Geoscience*, **6**, 268–273.

Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E. *et al.* (2004) Convergence across biomes to a common rain-use efficiency. *Nature*, **429**, 651–654.

IPCC (2014) *Fifth Assessment Report (AR5), Climate Change 2014: Synthesis Report*. Tech. rep, The Intergovernmental Panel on Climate Change, IPCC, Geneva, Switzerland.

Iverson, L.R. & Prasad, A.M. (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*, **68**, 465–485.

Keith, H., Mackey, B.G. & Lindenmayer, D.B. (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences*, **106**, 11635–11640.

Kempes, C.P., West, G.B., Crowell, K. & Girvan, M. (2011) Predicting maximum tree heights and other traits from allometric scaling and resource limitations. *PLoS ONE*, **6**, e20551.

King, D.A., Davies, S.J. & Noor, N.S.M. (2006) Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *Forest Ecology and Management*, **223**, 152–158.

Koven, C.D. (2013) Boreal carbon loss due to poleward shift in low-carbon ecosystems. *Nature Geoscience*, **6**, 452–456.

Liaw, A. & Wiener, M. (2002) Classification and Regression by randomForest. *R News*, **2**, 18–22.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

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.

Mascaro, J., Asner, G.P., Knapp, D.E., Kennedy-Bowdoin, T., Martin, R.E., Anderson, C., Higgins, M. & Chadwick, K.D. (2014) A tale of two "forests": random Forest machine learning aids tropical forest carbon mapping. *PLoS ONE*, **9**, e85993.

Michaletz, S.T., Cheng, D., Kerkhoff, A.J. & Enquist, B.J. (2014) Convergence of terrestrial plant production across global climate gradients. *Nature*, **512**, 39–43.

Ministère de l'Environnement (1996) IEFN: Inventaire Ecologique Forestier National. Tech. rep., Ministère de l'Environnement de Madagascar, Direction des Eaux et Forêts, DFS Deutsch Forest Service GmbH, Entreprise d'études de développement rural "Mamokatra", FTM.

Mitchard, E.T., Feldpausch, T.R., Brienen, R.J., Lopez-Gonzalez, G., Monteagudo, A., Baker, T.R. *et al.* (2014) Markedly divergent estimates of amazon forest carbon density from ground plots and satellites. *Global Ecology and Biogeography*, **23**, 935–946.

NASA Land Processes Distributed Active Archive Center (LP DAAC) (2014) *MODIS MOD13Q1 Version 005*. USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, SD, USA.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E. & McMurtrie, R.E. (2010) CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences*, **107**, 19368–19373.

ONE, DGF, FTM, MNP, CI (2013) *Evolution de la couverture de forêts naturelles à Madagascar 2005–2010*, Antananarivo.

Ouédraogo, D.Y., Mortier, F., Gourlet-Fleury, S., Freycon, V. & Picard, N. (2013) Slow-growing species cope best with drought: evidence from long-term measurements in a tropical semi-deciduous moist forest of Central Africa. *Journal of Ecology*, **101**, 1459–1470.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A. *et al.* (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Perry, L.G., Shafroth, P.B., Blumenthal, D.M., Morgan, J.A. & LeCain, D.R. (2013) Elevated CO_2 does not offset greater water stress predicted under climate change for native and exotic riparian plants. *New Phytologist*, **197**, 532–543.

Poorter, L., Bongers, L. & Bongers, F. (2006) Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology*, **87**, 1289–1301.

Powell, T.L., Galbraith, D.R., Christoffersen, B.O., Harper, A., Imbuzeiro, H., Rowland, L. *et al.* (2013) Confronting model predictions of carbon fluxes with measurements of amazon forests subjected to experimental drought. *New Phytologist*, **200**, 350–365.

Prentice, I.C., Bondeau, A., Cramer, W., Harrison, S.P., Hickler, T., Lucht, W., Sitch, S., Smith, B. & Sykes, M.T. (2007) Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. *Terrestrial ecosystems in a changing world* (eds J.G. Canadell, D.E. Pataki & L.F. Pitelka) pp. 175–192. Springer, Berlin, Germany.

Quillet, A., Peng, C. & Garneau, M. (2010) Toward dynamic global vegetation models for simulating vegetation-climate interactions and feedbacks: recent developments, limitations, and future challenges. *Environmental Reviews*, **18**, 333–353.

R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rakotovao, G., Rabevohitra, A., Gerad, J. & Collas de Chatelperron, P. (2011) *Atlas des bois de Madagascar*. Tech. rep, Fofifa and Cirad.

Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W. *et al.* (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences*, **108**, 9899–9904.

Scheiter, S., Langan, L. & Higgins, S.I. (2013) Next-generation dynamic global vegetation models: learning from community ecology. *New Phytologist*, **198**, 957–969.

Schimel, D., Pavlick, R., Fisher, J.B., Asner, G.P., Saatchi, S., Townsend, P., Miller, C., Frankenberg, C., Hibbard, K. & Cox, P. (2015) Observing terrestrial ecosystems and the carbon cycle from space. *Global Change Biology*, **21**, 1762–1776.

Sitch, S., Huntingford, C., Gedney, N., Levy, P., Lomas, M., Piao, S. *et al.* (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (dgvms). *Global Change Biology*, **14**, 2015–2039.

van der Sleen, P., Groenendijk, P., Vlam, M., Anten, N.P.R., Boom, A., Bongers, F., Pons, T.L., Terburg, G. & Zuidema, P.A. (2015) No growth stimulation of tropical trees by 150 years of CO_2 fertilization but water-use efficiency increased. *Nature Geoscience*, **8**, 24–28.

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.

Tadross, M., Randriamarolaza, L., Rabefitia, Z. & Ki Yip, Z. (2008) Climate change in Madagascar; recent past and future. Tech. rep, World Bank.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, **102**, 8245–8250.

Tollefson, J. (2013) Experiment aims to steep rainforest in carbon dioxide. *Nature*, **496**, 405–406.

Vieilledent, G., Grinand, C. & Vaudry, R. (2013b) Forecasting deforestation and carbon emissions in tropical developing countries facing demographic expansion: a case study in Madagascar. *Ecology and Evolution*, **3**, 1702–1716.

Vieilledent, G., Vaudry, R., Andriamanohisoa, S.F.D., Rakotonarivo, O.S., Randrianasolo, H.Z., Razafindrabe, H.N., Rakotoarivony, C.B., Ebeling, J. & Rasamoelina, M. (2012) A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. *Ecological Applications*, **22**, 572–583.

Vieilledent, G., Cornu, C., Cuni Sanchez, A., Leong Pock-Tsy, J.M. & Danthu, P. (2013a) Vulnerability of baobab species to climate change and effectiveness of the protected area network in Madagascar: towards new conservation priorities. *Biological Conservation*, **166**, 11–22.

Vieilledent, G, Gardi, O, Grinand, C, Burren, C., Andriamanjato, M., Camara, C., Gardner, C., Glass, L., Rasolohery, A., Ratsimba, H., Gond, V. & Rakotoarijaona, J.R. (2016) Data from: Bioclimatic envelope models predict a decrease in tropical forest carbon stocks with climate change in Madagascar. *Dryad Digital Repository*. http://dx.doi.org/10.5061/dryad.9ph68.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Wagner, F., Rossi, V., Aubry-Kientz, M., Bonal, D., Dalitz, H., Gliniars, R., Stahl, C., Trabucco, A. & Herault, B. (2014) Pan-tropical analysis of climate effects on seasonal tree growth. *PLoS ONE*, **9**, e92337.

van der Werf, G.R., Morton, D.C., DeFries, R.S., Olivier, J.G.J., Kasibhatla, P.S., Jackson, R.B., Collatz, G.J. & Randerson, J.T. (2009) CO_2 emissions from forest loss. *Nature Geoscience*, **2**, 737–738.

Zelazowski, P., Malhi, Y., Huntingford, C., Sitch, S. & Fisher, J.B. (2011) Changes in the potential distribution of humid tropical forests on a warmer planet. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **369**, 137–160.

Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, **18**, 1042–1052.

Received 19 August 2015; accepted 21 January 2016
Handling Editor: Emily Lines

Supporting Information

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

Figure S1. Height-diameter relationship by forest type.

Figure S2. Comparison between ACD observations and model predictions.

Figure S3. Predicted climatic anomalies between years 2010 and 2080 in Madagascar forests.

Table S1. Forest carbon stock projections using seven IPCC CMIP5 global climate models.