


REGULAR ARTICLE

The importance of soils in predicting the future of plant habitat suitability in a tropical forest

G. Zuquim  · F. R. C. Costa · H. Tuomisto ·
G. M. Moulatlet · F. O. G. Figueiredo

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Abstract

Aims Assessment of the future of biodiversity under climate change has been based on climate-only models. We investigated the effects of including soil information when predicting future suitable areas for selected plant species in Amazonia.

Methods We modelled current and future suitable habitats for 35 plant species and compared results of climate-only models with those obtained when climatic and edaphic variables were included. We considered six climatic scenarios for 2050 using different algorithms and projections of atmospheric CO₂ concentration.

Results Twenty-five species distribution models had an AUC > 0.69. Out of those, edaphic variables had the

greatest contribution in 11 species models, while climatic variables were more important for 14 species. The inclusion of soil variables affected the size and shape of predicted suitable areas, especially in future models. For nearly half of the species, the size of future suitable areas were smaller in climate+soil models than predicted by climate-only models. Area reduction was more extreme in future scenarios with the higher level of CO₂ concentration.

Conclusions Our results highlight the importance of moving beyond climatic scenarios when modelling biodiversity responses to climate change. Failure to include soils in the models can overestimate future habitat suitability for many plant species.

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G. Zuquim (✉) · H. Tuomisto
Department of Biology, University of Turku, Finland, FI-20014,
Turun Yliopisto, Turku, Finland
e-mail: gabriela.zuquim@utu.fi

F. R. C. Costa · F. O. G. Figueiredo
Coordination of Biodiversity Research, National Institute of
Amazonian Research, Av. André Araújo, 2936 - Petrópolis,
Manaus, AM 69067-375, Brazil

G. M. Moulatlet
Universidad Regional Amazónica – Ikiam, Vía Tena, Muyuna
Kilómetro 7, Tena, Ecuador

Keywords Climate change · Species distribution
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Abbreviations

GBIF	Global biodiversity information facility
IDigiBio	Integrated digitized biocollections
CMIP5	Coupled model intercomparison project phase 5
RCP	Representative concentration pathways
PPBio	Brazilian research program on biodiversity
RADAM	Amazonian radar project
BAU	Business-as-usual
GOV	Governance
CEC	Cation exchangeable capacity
AUC	Area under the curve
AIC	Akaike information criterion

Introduction

Climate, soil and dispersal capacity are the main natural determinants of current plant species distributions across the globe. Recent changes in climatic conditions are already affecting diversity patterns and ecosystem functioning, highlighting the pressure for species migration to meet their climatic niche requirements (Walther et al. 2002; Parmesan and Yohe 2003; Dillon et al. 2010; Pecl et al. 2017). Such effects are expected to increase during this century (Thomas et al. 2004) which reinforces the need for a research agenda focused on future biodiversity scenarios (Bellard et al. 2012; Lenoir and Svenning 2015; Poloczanska et al. 2013; Gruner et al. 2017).

Amazonia harbors the largest remaining area of tropical forest in the world and provides important ecosystem services that are heavily threatened by anthropogenic activities, particularly deforestation and global warming (Herraiz et al. 2017). Climate change scenarios predict drier and warmer future conditions for much of the Amazon region (Boisier et al. 2015; Cox et al. 2013; Spracklen et al. 2012) and drought-related fires have already become more frequent (Aragão et al. 2018). Climate projections for tropical areas have predicted a general increase in climate anomalies such as El Niño y La Niña events (Marengo and Espinoza 2016), rise of temperatures by up to 8 °C over the twenty-first century (Betts et al. 2008) and enhanced drought periods (Malhi et al. 2008). The drier and hotter future climate predicted for Amazonia (Betts et al. 2008) could drive a contraction in many species ranges, given that Amazonian plant species tend to be adapted to moist rainforest conditions and, hence, are sensitive to drought (Esquivel-Muelbert et al. 2017a, b; Nepstad et al. 2007).

In theory, the biological response to climate change can be either that i) species shift their distributions and migrate to suitable climate conditions (Feeley et al. 2011a, b), ii) species perish because they cannot tolerate the new climatic conditions and are unable to migrate or iii) species have sufficient phenotypic plasticity to cope with the climate change (Bush et al. 2016). Estimates of climatic tolerances of species and populations are difficult to determine, as well as migration and evolutionary rates. Nonetheless, ecological niche models predict that many species are to experience severe habitat loss and possible extinction (Miles et al. 2004) and the future of a species greatly depends on its abilities to thermal adaptation and migration (Feeley et al. 2012). Moreover,

long-term inventories showed that dry-affiliated tree genera are becoming more common in Amazonia, even though recruitment rates are probably slower than the trends in climate change (Esquivel-Muelbert et al. 2018).

Assessment of the future of global biodiversity using ecological niche modelling have proved to be an useful and intuitive framework. However, potential effects of climate change on species distribution has, so far, been based mainly on climate-only models (Bellard et al. 2012). Given that the effects of climate change on forest structure and species survival can vary along topographic gradients (Levine et al. 2016), species migration may be constrained by soil suitability in their potential migration pathway. Soils may filter species establishment through nutrient availability (Cámara-Leret et al. 2017; Tuomisto et al. 2016; Zuquim et al. 2012), water retention properties (Schietti et al. 2014), root-limiting physical conditions (Emilio et al. 2014), and biotic interactions conditioned by soil properties (Fine et al. 2004; Bever et al. 2010). If soils are not suitable for the species, the area is outside its niche tolerance and with low probability of its occurrence, regardless of climatic conditions. Therefore, climate-only ecological niche models are conceptually weak (Velazco et al. 2017) and their respective spatial predictions may be unreliable.

Investigating the future spatial distribution of niches that are analogous to current niche occupied by species is determinant to biodiversity conservation in the mid-term. To achieve reliable models, environmental preferences of the species should be properly represented. It is well documented that Amazonian forests vary considerably in soil and hydrology conditions as well as in species composition and vegetation structure (Tuomisto et al. 2003; Quesada et al. 2010; Higgins et al. 2011; Zuquim et al. 2012; Baldeck et al. 2016). Most plant species distributions in Amazonia that have been studied in detail have been found to be strongly affected by soil characteristics (Gentry 1988; Tuomisto and Poulsen 1996; Figueiredo et al. 2018). Therefore, models aiming to predict future habitat suitability should include soil conditions as well as climate.

One also needs caution when modelling future species suitable areas that large differences exist among predictions of future climatic conditions. To incorporate uncertainties and provide not one, but several climatic scenarios, 20 modelling groups promoted a set of coordinated climate model experiments known as Coupled Model Intercomparison Project phase 5 (CMIP5). The ensembled

climatologies differ in their input algorithms and in the assumptions about if and when the atmospheric CO₂ concentration peaks and starts to decline. The CO₂ emission scenarios considered a wide range of possibilities in future anthropogenic greenhouse gas emissions, reflecting the climatic policies adopted, if any (Moss et al. 2010; van Vuuren et al. 2011a).

The impact of other factors than climate on plant dispersal to and establishment in environmentally suitable areas may increase the negative climate effect of global warming on biodiversity. We thus aimed to understand to what degree taking soils into account affects the modelled availability of habitats for selected plant species given several scenarios of future climatic conditions in Amazonia.

Methods

Plant data

We compiled occurrence data for 35 species of herbs, lianas, trees and palms from biodiversity platforms (Global Biodiversity Information Facility - GBIF; Integrated Digitized Biocollections - IDigiBio); herbaria located in Brazil (INPA, IAN and MG) and USA (NY and MBG), and from plot-based inventories (Brazilian Research Program on Biodiversity - PPBio and RADAM-Brasil). Pre-modelling procedures consisted of removing geographical outliers and duplicated records, and reducing spatial bias (as described in Figueiredo et al. 2018). The 35 species were selected to cover a broad variability in plant size, life history strategies and phylogeny. We targeted species that are easy to identify in the field to avoid taxonomical errors. The list of the selected species is presented in Figueiredo et al. (2018 - Table 1), except that we left out all fern species. Exclusion of fern species was done to avoid circularity, given that the same fern records were used to develop the map of soil base cation concentration used for modelling (see next section). We also excluded *Eperua falcata*, whose GBIF records contained misidentified *Eperua leucantha* (ter Steege, personal communication).

Environmental variables

Soils We obtained soil Cation Exchange Capacity at pH 7 (CEC) and 5 cm depth from SoilGrids (soilgrids.org - downloaded in December 2016), which provides the data at 250 m resolution (Hengl et al. 2017). Because CEC is the only easily available high-resolution GIS layer that is related to soil nutrients, it has been applied in ecological studies in the tropics (Figueiredo et al. 2018; Levis et al. 2017; McMichael et al. 2014; Poorter et al. 2015). However, the usefulness of CEC to model plant communities in Amazonia is questionable (Moulatlet et al. 2017; Zuquim et al. 2017), because CEC is not a measure of current nutrient availability, but rather a measure of how well the soil is able to retain cations. The use of CEC is particularly problematic in Amazonia, where more than 90% of CEC is often occupied by aluminum (Quesada et al. 2011), which is not a plant nutrient. Therefore, we used a recently produced digital map of soil Exchangeable Base Cation Concentration (K, Mg, Ca) (Zuquim 2017) as an indicator of soil nutrient conditions for plants in natural vegetation (Moulatlet et al. 2017). This layer was developed by compiling field measurements of exchangeable base concentration from several databases and combining them with indirect cation concentration estimates based on the occurrence of indicator plant species (Zuquim et al. 2014). The compiled data were interpolated using ordinary kriging in pixels of 6 arcmin (~11 × 11 km) and validated with 194 soil samples of the RAINFOR project (Zuquim 2017; Zuquim et al., *in review*).

Climate We obtained current estimates of Annual Mean Temperature, Temperature Annual Range, Mean Temperature of Coldest Quarter, Annual Precipitation, Precipitation Seasonality and Precipitation of Driest Quarter (bio1, 7 12, 15 and 17) from Climatologies at high resolution (30 arcsec pixels) for the earth's land surface areas (CHELSA). CHELSA makes available future climate layers for 2050 based on five prediction models of the Coupled Model Intercomparison Project Phase 5 (CMIP5) from the last Intergovernmental Panel on Climate Change report. CMIP5 are multimodel ensemble simulations that provide robust estimates of future climatic conditions (Sillmann et al. 2013). The different climate scenarios are interdependent and contain similar biases, simplifications, parameterizations of processes, but they produce different climatic outputs. We therefore included high resolution models from CHELSA based on results from 5 different climatology research groups: Euro-Mediterranean Center on Climate Change (CMCC), Community Earth System Model (CESM),

Model for Interdisciplinary Research on Climate (MIROC), Max-Planck Institute Earth System Model (MPI-ESM) and Institut Pierre Simon Laplace (IPSL). These models were selected in order to cover a wide range of variation and they are well spread in the climate model genealogy (Knutti et al. 2013). Models from MPI (MPI-ESM-MR) and IPSL (IPSL-CM5A-LR) produced artifactual North-South straight lines and their results are not reported. Nevertheless, the remaining three models applied here were in extreme nodes of the climate model genealogy and, therefore, are expected to collectively represent the range of possible future climatic conditions well.

We also accounted for two different Representative Concentration Pathways (RCP) for Greenhouse gas concentration trajectories. RCP 8.5 is a baseline scenario that assumes no climate policy and, thus, emissions would continue to rise throughout the twenty-first century. It models future climatic conditions based on the projection of the current trends in economy, demography and energy use, without any specific climate mitigation target (Riahi et al. 2011). RCP 8.5 future models are hereafter referred to as business-as-usual (BAU) scenarios.

RCP 4.5 is an optimistic but still achievable scenario as it assumes that CO₂ concentration will peak around 2040 and then decline as a consequence of governmental incentive policies to lower carbon emission and concentration, e.g. cleaner energy technologies, carbon capture and geologic storage, and forest land expansion (Thomson et al. 2011). RCP 4.5 is hereafter referred to as the governance (GOV) scenarios.

We did not include RCP 2.6 scenarios, because they assume that CO₂ concentration peaks between 2010 and 2020 with emissions declining substantially thereafter (van Vuuren et al. 2011a). These scenarios depend on massive improvements in energy efficiency, reduced use of fossil fuels and massive implementation of negative emission technologies (van Vuuren et al. 2011b), which have been largely absent from climate policy actions so far (Anderson and Peters 2016). Moreover, the trend in CO₂ concentration from 1958 to 2018 has been a steady linear increase (Keeling and Keeling 2017) and there is no reason to believe this trend to change in the short window from now to 2020.

In summary, we used six climatic scenarios for 2050, divided into two major groups. One group contains three scenarios that assume a reduction in CO₂ emissions due to governance climatic policies (GOV) and the other group contains three scenarios that assume business-

as-usual emission rates (BAU). Each of the three scenarios in each group was produced by a different research team (CMCC-CMS, MIROC5 and CESM1-BGC) that considered different algorithms and climatological assumptions.

Data analysis

All environmental layers were re-scaled to an approx. 5 km × 5 km grid for analysis. We then run MaxEnt models to construct presence-background current species distribution models for 35 species of trees, lianas, monocot herbs, and palms. To achieve a balance between goodness-of-fit and predictive ability, we tuned MaxEnt model settings for each species (Merow et al. 2013; Syfert et al. 2013; Warren et al. 2014; Halvorsen et al. 2016) by running 32 models per species representing combinations of the features Linear, Linear-Quadratic, Linear-Quadratic-Product and Linear-Quadratic-Hinge with eight regularization multipliers (values from 0.5 to 4 at 0.5 intervals). We selected the combination of settings that produced models with the lowest value of Akaike information criterion with a correction for small sample sizes (AICc) for each species. We established a minimum value of full Area Under the Curve (AUC based on the full dataset) of 0.69 to consider the model adequate to be included in further analysis. To obtain maps of habitat suitability under future climatic conditions, we used the modelled species-environment relationships for current conditions and replaced the current climatic data with the projected climatic conditions in 2050 for spatial prediction.

All models were run separately using two different sets of environmental layers, one including five bioclimate layers only (hereafter, climate-only models) and the other including five climate layers and two soil layers (hereafter, climate+soil models). Climate-only and climate+soil species distribution models were generated for each of the seven climatic scenarios (one for the current climate and six future scenarios). To calculate the predicted suitable area for present and future species distribution models, we generated binary ecological niche models by applying a threshold value on the occurrence probability for each of the MaxEnt models. Threshold value for each model was defined as the maximum training sensitivity plus specificity (Liu et al. 2013). We calculated the ratio of the predicted surface areas to quantify the differences in

the areas predicted by a) climate and climate+soil models; b) present and future models and c) governance and business-as-usual future models. The ratio between the compared predicted areas was logarithmically transformed (base 2), which converts the ratio to an index that is symmetric around zero and in which a 2-fold difference in the areas being compared always corresponds to one unit difference in index value. We also applied a one-way ANOVA with a posteriori Tukey-test to evaluate the differences between AUC of climate-only and climate+soil models and between the areas predicted by different climate model algorithms.

All the analyses were done in R environment, using the packages “raster” (Hijmans 2016) for raster manipulation and calculations, “dismo” (Hijmans et al. 2017) for building MaxEnt models, and “ENMeval” (Muscarella et al. 2014, 2017) for model evaluation. Data from GBIF and iDigBio were downloaded using the package “spocc” (Chamberlain 2016) and geographical outliers were removed with the package “biogeo” (Robertson 2016).

Results

Comparisons between climate-only and climate+soil models

Out of the 35 species assessed, 25 had its current distribution models considered satisfactory ($AUC \geq 0.69$; Table 1). Information on the models for the 10 species with $AUC < 0.69$ is presented in supplementary materials (Table S1) but the results of these models were not considered in the subsequent analyses.

In general, the AUC values of current species distribution models were rather similar whether, besides climate, soil variables were included or not (Table 1) and no significant difference was found between climate-only and climate+soil AUCs of the models (ANOVA $\text{diff} = 0.02$, $\text{adj.}p = 0.48$). For 14 out of 25 climate+soil current species distribution models, the variable with the highest relative importance was bioclimatic, and in 11 models, it was edaphic.

The sizes of climate-only and climate+soil modelled suitable areas (calculated based on the binary models) were correlated (Pearson's $r = 0.71$). The correlation between the sizes of suitable areas predicted by climate-only and climate+soil in future models varied

between 0.68 and 0.72 depending on the future scenario considered.

The inclusion of soil variables affected the size of predicted suitable areas based on binary maps. For nearly half of the species, climate-only models predicted larger future suitable areas than climate+soil models (Fig. 1).

A visual inspection of the maps suggests that the inclusion of soils affected not only the total suitable area, but also its spatial distribution, especially in the future predictions. For example, climate-only models predicted that the upper Rio Negro area in northwestern Brazil would become climatically suitable in 2050 for the palm *Iriartea deltoidea* (Fig. 2) and for the understory herb *Heliconia schumanniana* (Fig. 3). However, when soil variables were included in the model, low probability values were assigned to these same areas, possibly because of the extremely nutrient-poor soils that are found there. On the other hand, the Andean forelands were only predicted as suitable for *Iriartea deltoidea* when soils were taken into account. For the herb *Goeppertia fragilis* (Fig. 4) and the tree *Nectandra turbacensis* (Fig. 5), climate-only models clearly predicted larger suitable areas in the future than climate+soil models did, with the latter nested within the former. Finally, soil data contributed very little to the models of the liana *Macherium amplum*, and for this species the climate-only and climate+soil models were roughly similar (Fig. 6). The current and future suitability maps of the species that were not mentioned above are presented in the Supplementary material (Figs. S1–S20).

Comparison between present and future scenarios

Species that had their current suitable area reduced in the future according to climate+soil models, were predicted to have more extreme suitable-area losses under business-as-usual scenarios than under governance scenarios (Fig. 7, Table S2). *Heliconia schumanniana* (Fig. 3) is an example of a species whose suitable area is predicted to contract in the future, especially when soils are taken into account. Species suitable areas were reduced on average to between 1/7th and 1/10th of their current extent (corresponding to area index values between -2.8 and -3.3) under the business-as-usual scenarios (Fig. 7b,d), and to between 1/4th and 1/9th (corresponding to area index values between -2 and -3.2) under the governance scenarios (Fig. 7a,c).

Table 1 Details of the best distribution models based on current climatic conditions for each of the 25 Amazonian plant species as obtained with the maximum entropy algorithm (Maxent). Two models are shown for each species, one including bioclimatic variables (bio) only (Clim-only models), the other also including the concentration of exchangeable bases (“Nutrients”; the sum of Ca, Mg and K concentrations in the soil) and cation exchange capacity (CEC) of the soil (Clim+soil models). Species are sorted in order of decreasing contribution of Nutrients and then CEC to clim+soil models. Only species with AUC values >0.69 in at least one of the models are shown here; results for the other species are in Supplementary Table 1. The bioclimatic variables are annual mean temperature (“bio1”), temperature annual range (“bio7”),

annual precipitation (“bio12”), precipitation seasonality (“bio15”) and precipitation of driest quarter (“bio17”). For more details, see <http://chelsa-climate.org/bioclim/>. “Feature” refers to the mathematical transformations of covariates applied by models to allow complex relationships: linear (L), linear quadratic (LQ), linear-quadratic-product (LQP) and linear-quadratic-hinge (LQH). The regularization multiplier (“RM”) is the penalty weight on model complexity. Full AUC is the Area Under the Curve for models using the full occurrences dataset (as opposed to the mean AUC that is based on training datasets). The best model was defined as the one with the lowest value of Akaike information criterion with a correction for small sample sizes (AICc)

Species	bio1	bio7	bio12	bio15	bio17	Nutrients	CEC	Feature	RM	Full AUC	Model
<i>Monotagma ulei</i>	0.1	19.9	8	0.5	6.6	64.1	0.8	LQP	0.5	0.83	Clim+soil
	6.4	61.6	0	9.3	22.8	NA	NA	LQP	0.5	0.84	Clim-only
<i>Henriquezia nitida</i>	0	14.5	1	3	2.2	59.5	19.7	LQH	3	0.96	Clim+soil
	4.1	61.7	4.1	2.8	27.3	NA	NA	LQH	2.5	0.95	Clim-only
<i>Goeppertia zingiberina</i>	6	16.6	13.1	6.7	0.6	52.4	4.5	LQP	0.5	0.75	Clim+soil
	25.7	42.4	6.6	3	22.4	NA	NA	LQP	0.5	0.75	Clim-only
<i>Goeppertia fragilis</i>	7.4	20.7	1.3	1.4	13.9	48.1	7.2	LQP	0.5	0.87	Clim+soil
	0.1	20.7	0	31.3	47.9	NA	NA	LQP	0.5	0.85	Clim-only
<i>Leopoldinia pulchra</i>	5.5	2.3	1.9	4.9	7.6	43.5	34.3	LQP	1.5	0.89	Clim+soil
	0.5	74.8	7	12.1	5.5	NA	NA	LQP	2	0.88	Clim-only
<i>Machaerium ferox</i>	7.2	1.6	32.9	5.7	5.7	31.4	15.4	LQ	0.5	0.81	Clim+soil
	40.5	42	13.9	2.6	1	NA	NA	LQ	0.5	0.8	Clim-only
<i>Poecilanthe effusa</i>	1.8	10.9	39.3	5.9	3.8	30.4	7.9	LQP	1	0.71	Clim+soil
	44	42	4.2	1.6	8.1	NA	NA	LQ	0.5	0.69	Clim-only
<i>Manilkara huberi</i>	17.9	10.9	24.8	4.4	4	27.8	10.2	LQP	1	0.76	Clim+soil
	37.6	33.3	13.7	5.5	9.9	NA	NA	LQP	0.5	0.75	Clim-only
<i>Caryocar glabrum</i>	1.2	6.5	12.1	1.9	34.7	25.8	17.8	LQP	0.5	0.69	Clim+soil
	13.9	51.3	2.6	24.7	7.4	NA	NA	LQ	0.5	0.68	Clim-only
<i>Nectandra turbacensis</i>	6.8	0	8.3	0	0	22.5	62.4	L	2	0.83	Clim+soil
	0.9	99.1	0	0	0	NA	NA	L	2	0.72	Clim-only
<i>Caryocar microcarpum</i>	2.8	3.6	11.3	1.1	1.4	20.7	59	LQ	0.5	0.78	Clim+soil
	16.3	68.4	1.1	4.1	10.1	NA	NA	LQP	0.5	0.77	Clim-only
<i>Machaerium multifoliolatum</i>	4.7	10.7	6.2	0	49.4	20.4	8.6	L	1	0.71	Clim+soil
	0	8.2	0	91.8	0	NA	NA	L	3	0.66	Clim-only
<i>Machaerium amplum</i>	0	58.1	2.5	0	27.2	12.2	0	LQP	4	0.77	Clim+soil
	5.9	6.9	0.9	7.8	78.5	NA	NA	LQP	1.5	0.78	Clim-only
<i>Hylaeanthus hexantha</i>	1.8	9.5	21.5	20.9	6.7	11.7	27.9	LQP	1	0.79	Clim+soil
	11.6	28.5	24.6	18.9	16.3	NA	NA	LQP	0.5	0.74	Clim-only
<i>Couepia dolichopoda</i>	2.5	61.7	0	0	5.4	9.6	20.7	L	1	0.93	Clim+soil
	2.4	19.5	0	0	78.1	NA	NA	LQH	2	0.94	Clim-only
<i>Socratea exorrhiza</i>	7.1	31.5	6.4	1.4	34.4	6.5	12.6	LQ	0.5	0.73	Clim+soil
	6.9	12.1	4.3	30.6	46.1	NA	NA	LQP	0.5	0.72	Clim-only
<i>Heliconia schumanniana</i>	2.3	33.5	12.8	0.8	16.6	6.4	27.6	LQP	1.5	0.97	Clim+soil
	27.7	16.4	3.1	29.9	22.9	NA	NA	LQP	1	0.95	Clim-only
<i>Pleonotoma jasminifolia</i>	3.9	0	11.7	1	2.1	3.8	77.4	LQP	1.5	0.83	Clim+soil

Table 1 (continued)

Species	bio1	bio7	bio12	bio15	bio17	Nutrients	CEC	Feature	RM	Full AUC	Model
<i>Oenocarpus bataua</i>	11.6	67.4	14.3	2.4	4.3	NA	NA	LQP	0.5	0.78	Clim-only
	11	13.5	24.1	1	29.2	2.1	19.2	LQP	2	0.81	Clim+soil
	5	9.4	0.1	83.8	1.7	NA	NA	LQ	1	0.77	Clim-only
<i>Iriartea deltoidea</i>	21.4	20.7	12.7	0	16.1	0.9	28.2	LQH	3.5	0.83	Clim+soil
	10	31.6	2.4	31.8	24.2	NA	NA	LQP	1.5	0.82	Clim-only
<i>Martinella obovata</i>	38.1	2.3	14.2	0	45.2	0.2	0	L	3.5	0.71	Clim+soil
	2.8	3.5	0.1	88.8	4.8	NA	NA	LQP	1	0.68	Clim-only
<i>Renealmia breviscapa</i>	2.7	0.3	27	5.4	34.5	0	30	LQP	3.5	0.86	Clim+soil
	5.1	36.5	0.1	55.4	2.9	NA	NA	LQ	0.5	0.83	Clim-only
	0	11.6	43	2.5	8.7	0	34.1	LQ	3	0.91	Clim+soil
<i>Ischnosiphon martianus</i>	25	37.9	5	11.5	20.5	NA	NA	LQP	0.5	0.91	Clim-only
	0	46.5	10.4	0	33.8	0	9.3	LQ	3.5	0.74	Clim+soil
	41.4	7.8	0.4	20.8	29.6	NA	NA	LQP	1	0.75	Clim-only
<i>Rourea cuspidata</i>	0.2	0	4.4	0	89.9	0	5.5	L	3	0.9	Clim+soil
	9.9	4.8	0	56.6	28.7	NA	NA	LQH	1.5	0.91	Clim-only

In an extreme case, a species was predicted to have its area reduced to 1/315th (area index value -8.3) under a business-as-usual scenario and to 1/34th (area index value -5.1) under a governance scenario, in relation to current suitable area (Fig. 7). Suitable areas for *Couepia dolichopoda* (Fig. S3) and *Henriquezia nitida* (Fig. S6) were predicted to be reduced to practically zero under certain climate-only future scenarios. No suitable area was predicted for *Leopoldina pulchra* in the climate-only business-as-usual scenario of CMCC-CMS model (Fig. S9). On the other hand, for between 9 and 13 species, future conditions appear to provide more suitable area than current ones (Fig. 7), even when soils and climate are taken into account together (e.g. *Nectandra turbacensis*, Fig. 6).

Comparison among future scenarios

The predictions using three climatologies from different research groups were relatively consistent for the models with the same projected CO₂ concentration, even though models including CMCC-CM5 climate projections tended to predict slightly smaller suitable areas than when including CESM1-BGC or MIROC5 projections in the models (Fig. S21). However, for most of the plant species modelled, the predicted future suitability using business-as-usual

climate scenarios tended to predict less area than models using governance scenarios, regardless of the research group (Fig. 8).

Discussion

In this study we have found that 1) the projection of future habitat suitability of species based on climate-only models can considerably overestimate suitable areas for species with strong soil affinity; 2) at the same time, the inclusion of soil variables in our models increased the predicted suitable area in the future for other species, which can be considered good news for these species; 3) for half of the species, future suitable areas were predicted to be smaller than current ones if no climate policies are adopted; two of the species were predicted to have no future suitable area at all; 4) for some species inhabiting the fringes of Amazonia, larger suitable areas were predicted for the future; and 5) governance scenarios tended to predict larger suitable areas in the future than business-as-usual scenarios.

For species limited by soil conditions, we hypothesized that climate-only models would predict larger suitable areas in the future than when soils were also taken into account. Climatically suitable areas

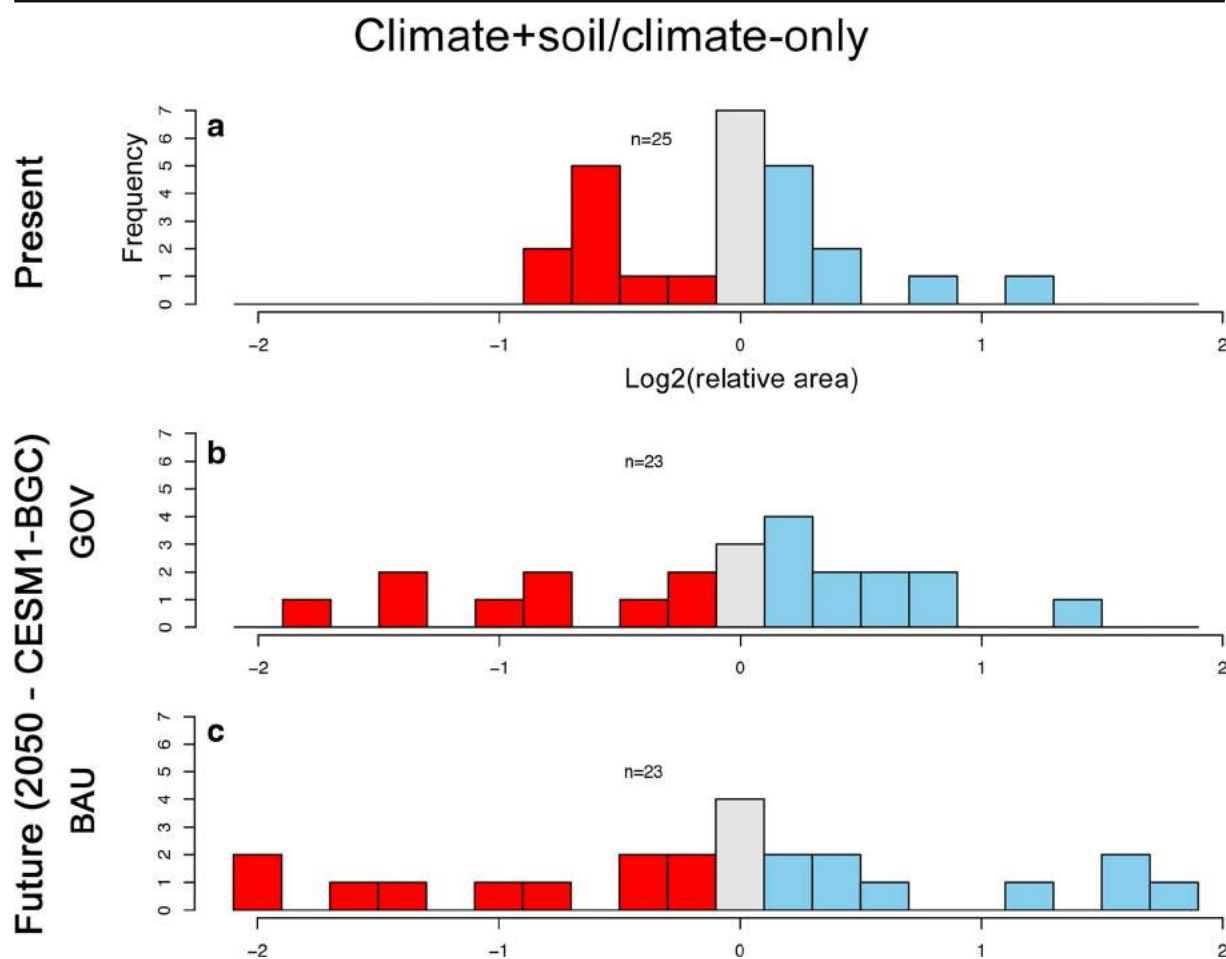


Fig. 1 Frequency histograms of the logarithmically transformed (base 2) ratio between the suitable areas as predicted using climate-only and climate+soil models for each of n plant species in Amazonia. Climatic variables were based either on present climate (a) or on climatic predictions for 2050 using CESM1-BGC Governance [GOV, (b)] and Business-as-usual [BAU, (c)] scenarios. Negative values (red) mean that the climate-only model predicted larger suitable areas than the climate+soil model for the same

species. Positive values (blue) mean that climate+soil model predicted larger suitable area than the corresponding climate-only model for the same species. Values close to zero (gray) correspond to species for which climate-only and climate+soil models predicted approximately equal suitable areas. Two species (*Henriquezia nitida* and *Couepia dolichopoda*) were predicted to have no suitable area under future climate conditions, and therefore are not included in (b) and (c)

for a species may have soils that are not adequate for its establishment. In addition, not only difference in the size of the areas where expected, but also, in the spatial configuration. In fact, that was observed for several species, e.g. *Renealmia breviscapa*, *Heliconia schumanniana* and *Iriarteia deltoidea*. For these three species, the upper Rio Negro region was predicted to be suitable by climate-only-models. However, the dominant soils in that area are more nutrient-poor than in the areas where these species are currently known to occur, which possibly makes the area unsuitable for them. Indeed, climate+soil

models did not predict the upper Rio Negro as a suitable area for these species in the future. According to these models, future suitable areas are concentrated along the Andean foreland, where soils tend to be richer in nutrients (Quesada et al. 2010).

Our results reinforce earlier findings that soils are important for the understanding of current species distributions in Amazonia (Tuomisto et al. 2016; Costa et al. 2009) and that the inclusion of soil variables can improve broad-scale species distribution models when compared to the performance of

Iriartea deltoidea

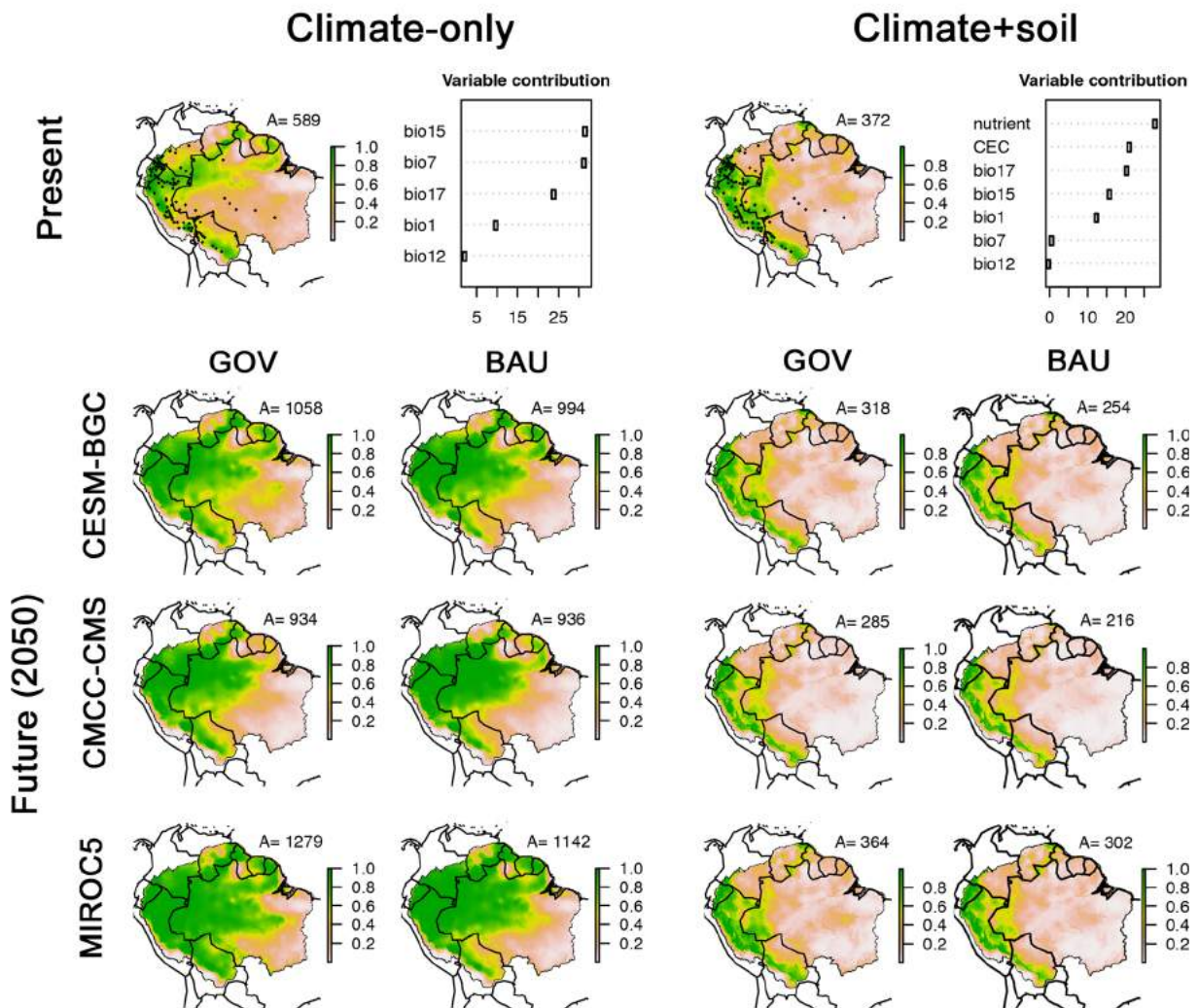


Fig. 2 Predictions of environmentally suitable areas for the occurrence of the palm *Iriartea deltoidea* using climate-only models (two first columns) and climate+soil models (two last columns). The first row presents the modelled habitat suitability under current environmental conditions (with black dots indicating species occurrence records), and the scatterplots of the relative contribution of each variable to the model (in %). For variable names in

full, see Table 1. Future models were based on climatologies developed by three different research groups (CESM1-BGC, CMCC-CMS and MIROC5) taking into account atmospheric CO₂ concentration scenarios under governance (GOV) and business-as-usual (BAU) climatic policies. The estimated suitable area (A, in 1000 km²) was estimated for each model after applying a threshold on the relative probability values

climate-only models (Figueiredo et al. 2018; Velazco et al. 2017). Species distribution models including remote sensing layers to represent vegetation properties (e.g. leaf area index, greenness, tree cover) have also been more successful than climate-only models (Buermann et al. 2008). This may ultimately also reflect the influence of soils, which can affect various forest properties (Quesada et al. 2012; Higgins et al.

2015) especially in areas where climate is relatively homogeneous. Consequently, appropriate representation of soil conditions should be included in any attempt to forecast future distributions of species. This is challenging because, even though considerable effort has been invested in producing digital soil maps that cover the entire world (Nachtergaele et al. 2012; Dijkshoorn et al. 2005; Hengl et al. 2017), in

Heliconia schumanniana

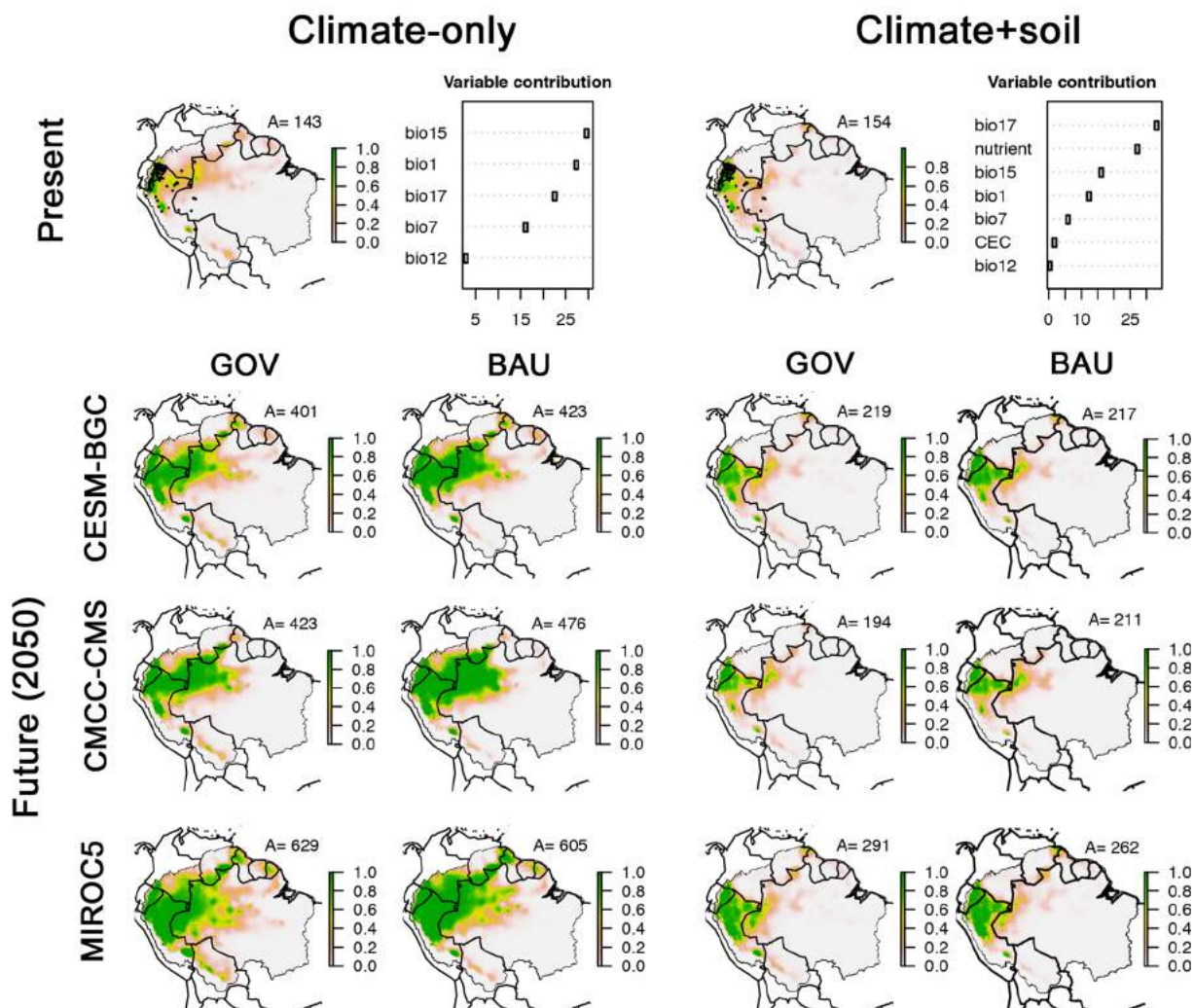


Fig. 3 Predictions of environmentally suitable areas for the occurrence of the understory herb *Heliconia schumanniana* using climate-only models (two first columns) and climate+soil models (two last columns). The first row presents the modelled habitat suitability under current environmental conditions (with black dots indicating species occurrence records), and the scatterplots of the relative contribution of each variable to the models (in %). For

variable names in full, see Table 1. Future models were based on climatologies developed by three different research groups (CESM1-BGC, CMCC-CMS and MIROC5) taking into account atmospheric CO₂ concentration scenarios under governance (GOV) and business-as-usual (BAU) climatic policies. The estimated suitable area (A, in 1000 km²) was estimated for each model after applying a threshold on the relative probability values

data-poor areas, such as Amazonia, these maps still suffer from serious inaccuracies (Moulatlet et al. 2017). We mitigated this problem by adding an exchangeable cation concentration map produced specifically for the Amazonian region (Zuquim 2017) and with a greater density of input data points when compared with global soil maps. This contributed to a better representation of environmental variation and

thus better current species distribution and future suitability models.

For few species, the total suitable areas predicted by climate+soil models were relatively similar for current and future scenarios. In some cases, the areas predicted by climate+soil models were even larger than climate-only predicted suitable areas for the future. This is probably because we assumed that

Goeppertia fragilis

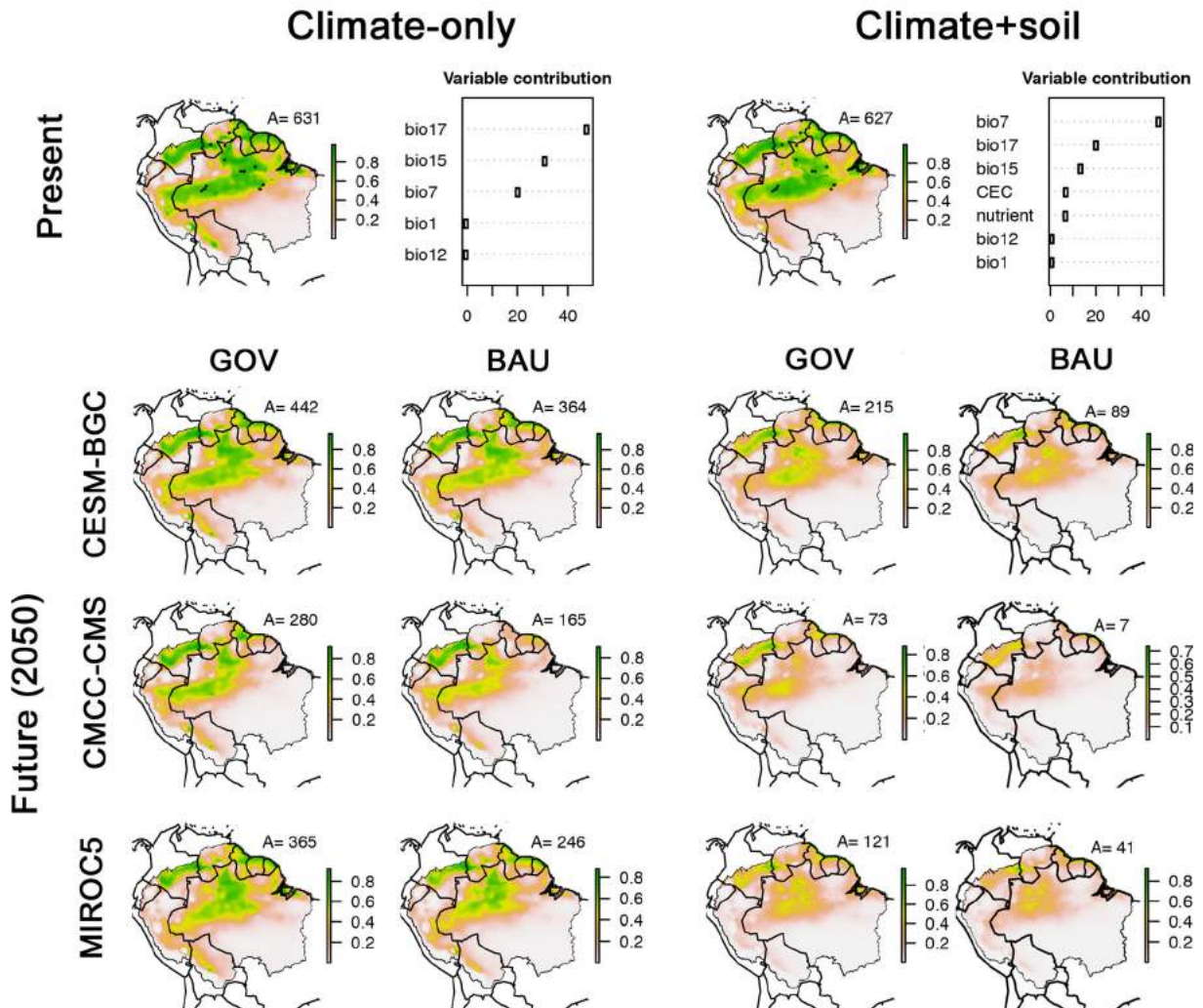


Fig. 4 Predictions of environmentally suitable areas for the occurrence of the understory herb *Goeppertia fragilis* using climate-only models (two first columns) and climate+soil models (two last columns). The first row presents the modelled habitat suitability under current environmental conditions (with black dots indicating species occurrence records), and the scatterplots of the relative contribution of each variable to the models (in %). For variable

names in full, see Table 1. Future models were based on climatologies developed by three different research groups (CESM1-BGC, CMCC-CMS and MIROC5) taking into account atmospheric CO₂ concentration scenarios under governance (GOV) and business-as-usual (BAU) climatic policies. The estimated suitable area (A, in 1000 km²) was estimated for each model after applying a threshold on the relative probability values

in the time scale modelled, soils will not change as fast as climate and thus, current and future soil conditions are similar. In this scenario, species that are more determined by soil than climate would be less prone to be affected by climate change. In any case, these models illustrate that climate-only models are incomplete when assessing future ranges of plant species.

In the long term, drought will likely cause biodiversity and biomass loss, since moisture availability partially constrains plant species richness (Kessler et al. 2011; Tuomisto et al. 2014; Esquivel-Muelbert et al. 2017a) and above-ground biomass (Saatchi et al. 2007). For nearly half of the species modelled here, the projected future suitable areas were smaller than current. Similarly, Miles et al. (2004) estimated

Nectandra turbacensis

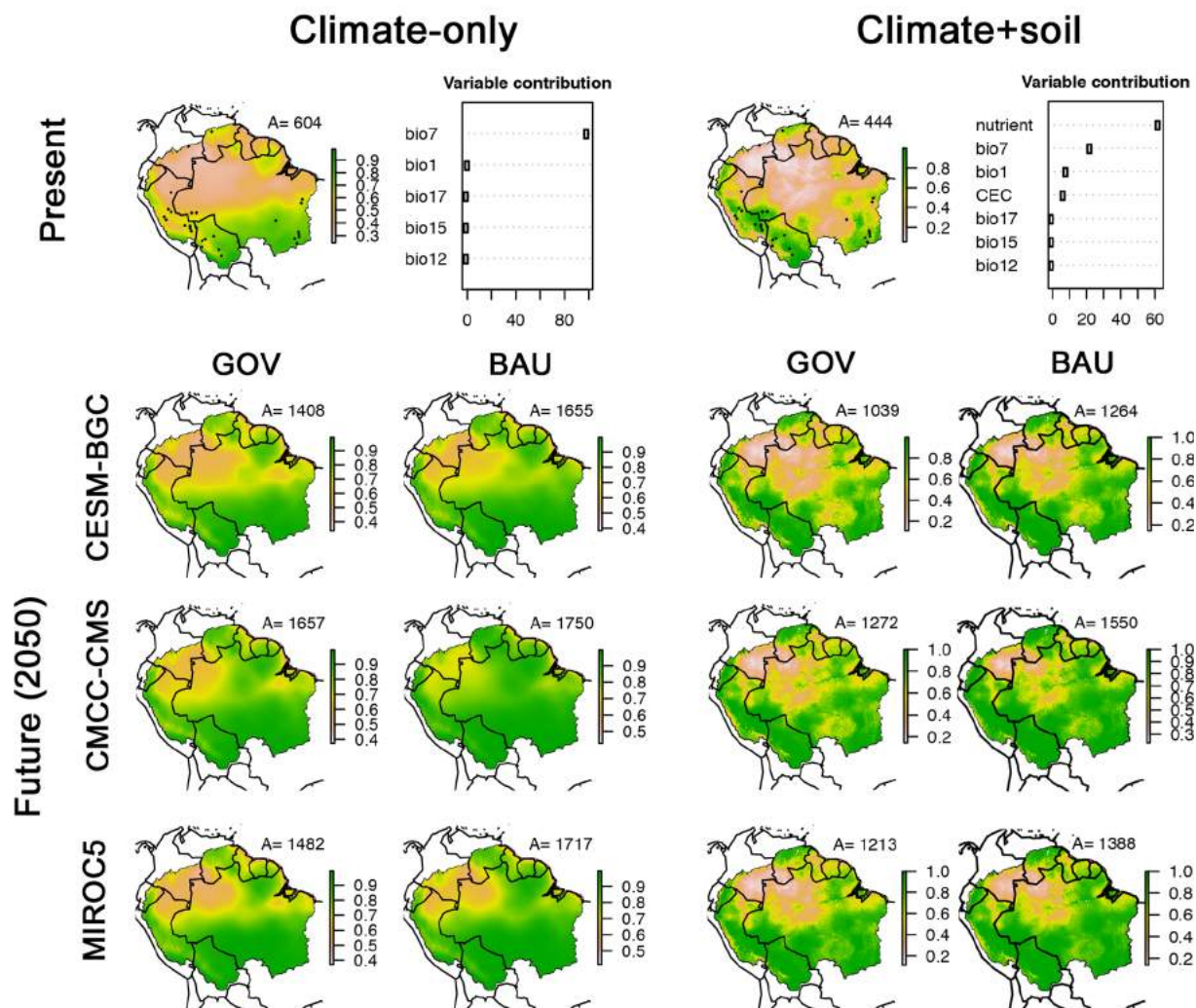


Fig. 5 Predictions of environmentally suitable areas for the occurrence of the tree *Nectandra turbacensis* using climate-only models (two first columns) and climate+soil models (two last columns). The first row presents the modelled habitat suitability under current environmental conditions (with black dots indicating species occurrence records), and the scatterplots of the relative contribution of each variable to the models (in %). For variable

names in full, see Table 1. Future models were based on climatologies developed by three different research groups (CESM1-BGC, CMCC-CMS and MIROC5) taking into account atmospheric CO₂ concentration scenarios under governance (GOV) and business-as-usual (BAU) climatic policies. The estimated suitable area (A, in 1000 km²) was estimated for each model after applying a threshold on the relative probability values

that 30 out of 69 Amazonian tree species populations would decrease in the future due to climate change. On the other hand, Feeley et al. (2012) have projected less dramatic loss of favorable areas for species in the future (8–12%), assuming that species have enough plasticity to adapt to rising temperatures in addition to migrating. Nevertheless, none of the previous studies properly assessed the constraints imposed by soil

specialization. Our models suggest that many species have smaller suitable areas in the future when soil limitations are taken into account. Therefore, the projected reduction in suitable areas, population sizes and species viability under climate change can be expected to be worse than projected before.

In our dataset, part of the species for which projected future suitable areas were larger than

Machaerium amplum

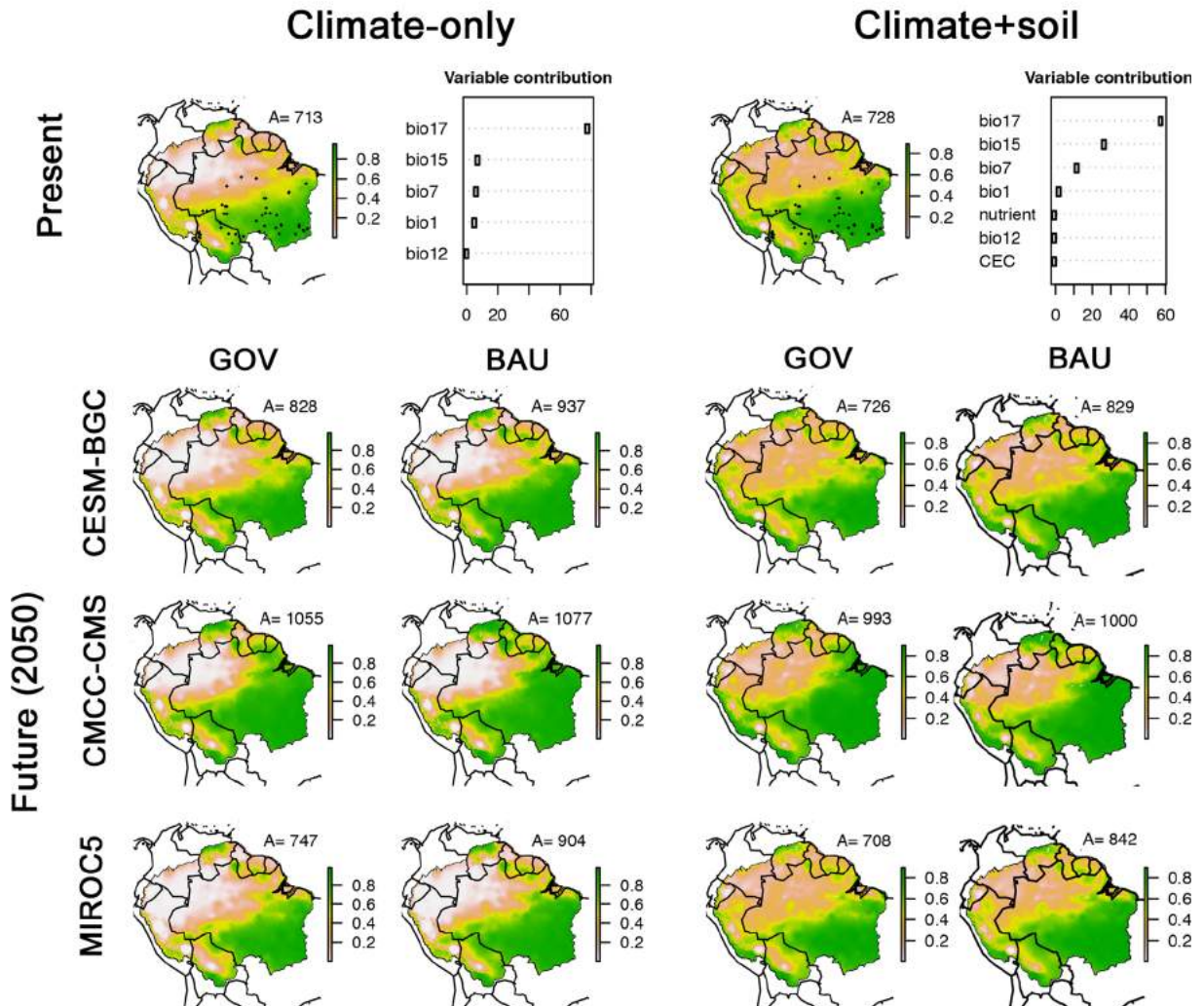


Fig. 6 Predictions of environmentally suitable areas for the occurrence of the liana *Machaerium amplum* using climate-only models (two first columns) and climate+soil models (two last columns). The first row presents the modelled habitat suitability under current environmental conditions (with black dots indicating species occurrence records), and the scatterplots of the relative contribution of each variable to the models (in %). For variable

names in full, see Table 1. Future models were based on climatologies developed by three different research groups (CESM1-BGC, CMCC-CMS and MIROC5) taking into account atmospheric CO₂ concentration scenarios under governance (GOV) and business-as-usual (BAU) climatic policies. The estimated suitable area (A, in 1000 km²) was estimated for each model after applying a threshold on the relative probability values

current ones currently inhabit the southern parts of Amazonia, in the Amazonia/Cerrado ecotone (e.g. *Nectandra turbacensis* and *Macherium multifoliolatum*). Given that this area is currently drier and more seasonal than core Amazonia, these species are already adapted to the conditions that are predicted to become more common in the basin (Marengo and Espinoza 2016; Betts et al. 2008).

In general, scenarios assuming future reduction in CO₂ emissions predicted larger suitable area for species in 2050 than the business-as-usual emission scenarios. It is worth noting that variation among predicted area using climatic models that assumes the same CO₂ emission scenarios but developed by different research groups also occurred. Therefore, uncertainty in the future of Amazonian climate should

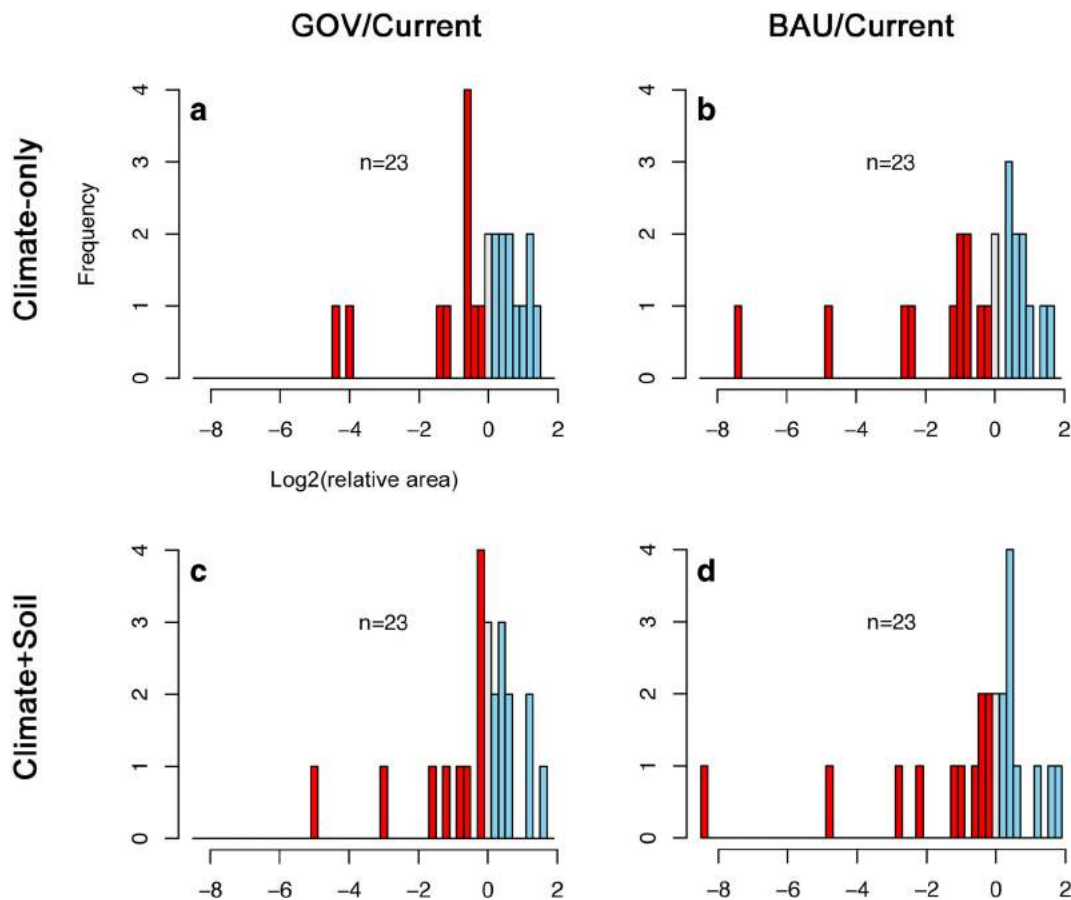


Fig. 7 Frequency histograms of the logarithmically transformed (base 2) ratio between the suitable areas as predicted for each of n plant species in Amazonia under future and current climate conditions for climate-only (**a**, **b**) and climate+soil models (**c**, **d**). Future climatic conditions presented are based on high-resolution CESM1-BGC climate projections for scenarios of atmospheric CO_2 concentrations under (**a**) and (**c**) governance (GOV) emission policies; and (**b**) and (**d**) business-as-usual (BAU) emission trends.

Negative values (red) correspond to species for which the current models predicted larger suitable areas than future models did. Positive values (blue) mean that the future model predicted larger suitable area than the current model for the same species. *Henriquezia nitida* and *Couepia dolichopoda* were predicted to have no suitable habitat under future climate conditions, and therefore were not included in the graphs

also be taken into account in predictions of the future of biodiversity and conservation actions.

The evaluation of the future distributions of Amazonian species presented here does not include other potential constraints to species migration towards favourable climates, such as deforestation, land-use change (Feeley et al. 2012; Manchego et al. 2017) or variation in species dispersal abilities (Engler et al. 2009; Willis and Bhagwat 2009). Several taxa may not be able to disperse fast enough to track the changes in suitable areas spatial distribution (Esquivel-Muelbert et al. 2018). This may reduce species ranges by imposing limits to migration. In particular, many shrubs and herbs

have limited dispersal ability, so their future distribution areas can be expected to be smaller than the areas providing suitable habitat (Nekola and White 1999; Hubbell 2001). The same is probably true for any plant species whose dispersal is highly dependent on animals with small home ranges. On the other hand, species may have enough acclimation potential to cope with conditions that they do not currently tolerate, but the degree to which this may happen is unknown. Further research is needed to clarify the synergistic effects of soil barriers, land-use change, climate, dispersal ability and potential adaptation on the future of Amazonian species.

Future: BAU/GOV

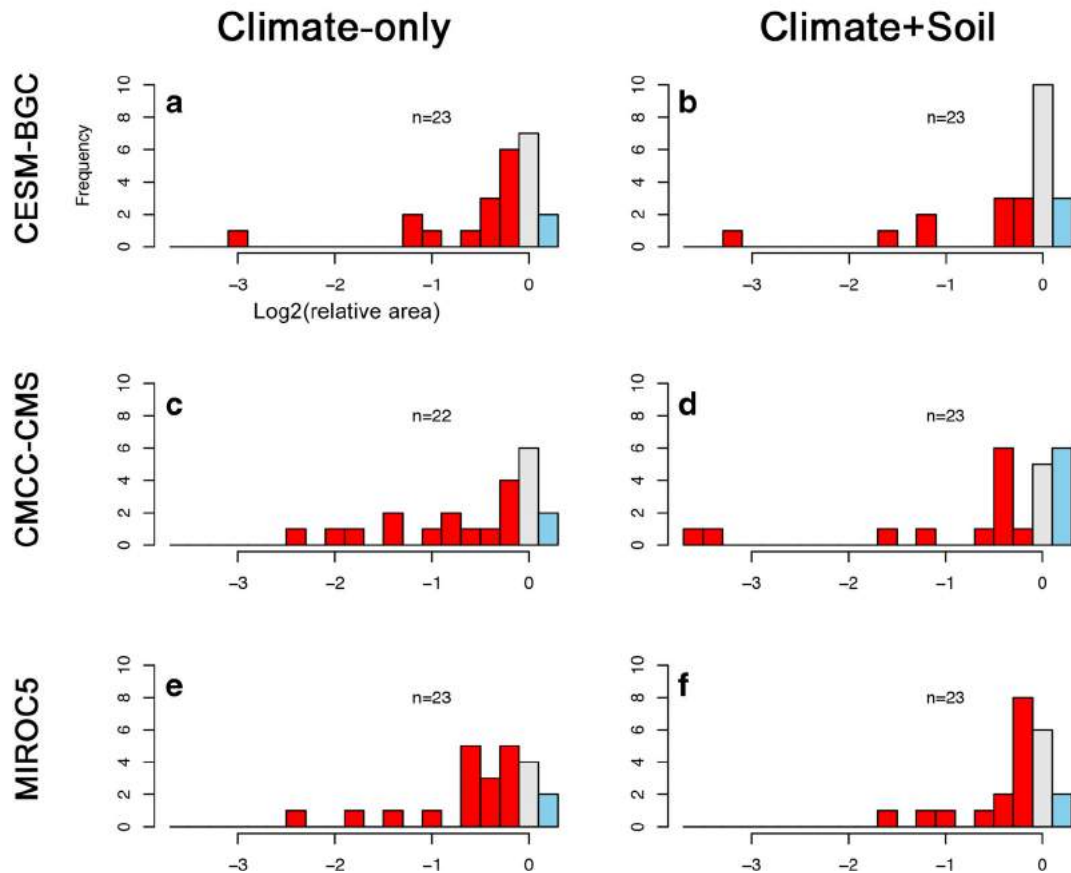


Fig. 8 Frequency histograms of logarithmically transformed (base 2) ratio between suitable area predicted using two scenarios of CO₂ concentration peak and decline for *n* plant species in Amazonia. Climatic scenarios resulting from governance (GOV) and Business-as-usual (BAU) policies were obtained based on three different climate projections [CESM1-BGC (a, b), CMCC-CMS (c, d) and MIROC5 (e, f)]. Climate-only species distribution models are shown at left (a, c, e) and climate+soil models at right

(b, d, f). Negative values (red) correspond to species for which GOV models predicted larger suitable area than BAU models for the same species. Positive values (blue) mean that the BAU future models predicted larger suitable area than the GOV model for the same species. *Henriquezia nitida*, *Couepia dolichopoda* and *Leopoldinia pulchra* were predicted to have no suitable habitat under certain future climate conditions, and were therefore not included in the graphs

Conclusions

Our results highlight the importance of moving beyond climatic scenarios when modelling biodiversity responses to climate change. Climate-only models are incomplete (Figueiredo et al. 2018; Velazco et al. 2017) and may overestimate future suitability of areas for several species. Species with distributions strongly determined by soil conditions have smaller future suitable areas than climate-only models can predict, especially if the soil conditions to which the species is specialized have limited distribution in

Amazonia. These observations are probably true for the larger Amazonian flora, given that strong plant-soil associations have already been described for almost every plant group (Costa et al. 2009; Tuomisto et al. 2016).

Even though our models suggested significant area reduction and even pointed out to possible species extinctions, our results might still be considered optimistic given that rare species or species with small ranges were not included. The conservation status of trees, for instance, is already alarming; many species with small populations

can be compromised by 2050 (ter Steege et al. 2015). Therefore, estimating species suitable areas on the basis of models that include the main environmental drivers of species distribution is crucial for planning conservation areas that mitigate the effects of climate change on biodiversity. In the predicted more seasonal and hotter future, a large part of the Amazonian flora may not be able to track suitable climates due to soil barriers in between migration pathways. The inclusion of other factors such as dispersal limitation, habitat loss and fragmentation might reveal an even worse scenario. In any case, the future of Amazonian biodiversity is worrisome.

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Author contribution GZ and FF conceived the study. GZ analysed the data with support from HT and FF. GZ and FC led the writing. All authors contributed with data, ideas and writing the manuscript.

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