

The relative importance of deforestation, precipitation change, and temperature sensitivity in determining the future distributions and diversity of Amazonian plant species

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Abstract

Tropical forests are threatened by many human disturbances – two of the most important of which are deforestation and climate change. To mitigate the impacts of these disturbances, it is important to understand their potential effects on the distributions of species. In the tropics, such understanding has been hindered by poor knowledge of the current distributions and range limits of most species. Here, we use herbarium collection records to model the current and future distributions of ca. 3000 Amazonian plant species. We project these distributions into the future under a range of different scenarios related to the magnitude of climate change and extent of deforestation as well as the response of species to changes in temperature, precipitation, and atmospheric concentrations of CO₂. We find that the future of Amazonian diversity will be dependant primarily on the ability of species to tolerate or adapt to rising temperatures. If the thermal niches of tropical plant species are fixed and incapable of expanding under rapid warming, then the negative effects of climate change will overshadow the effects of deforestation, greatly reducing the area of suitable habitat available to most species and potentially leading to massive losses of biodiversity throughout the Amazon. If tropical species are generally capable of tolerating warmer temperatures, rates of habitat loss will be greatly reduced but many parts of Amazonia may still experience rapid losses of diversity, with the effects of enhanced seasonal water stress being similar in magnitude to the effects of deforestation.

Keywords: biodiversity informatics, extinction, global warming, natural history collections, species distribution models, species migrations

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Introduction

The distributions of species are predicted to shift, or ‘migrate’, under climate change (Thuiller, 2007; Walther *et al.*, 2002). This prediction is supported by paleo-ecological studies showing shifts in species’ historical ranges concurrent with past climate changes (Bush *et al.*, 2004; Petit *et al.*, 2008) as well as a growing number of recent studies showing shifts in modern species distributions (e.g., Bertrand *et al.*, 2011; Chen *et al.*, 2011; Crimmins *et al.*, 2011; Feeley, 2012; Feeley *et al.*, 2011; Forero-Medina *et al.*, 2011; Parmesan, 2006).

Distributional shifts will be especially important for tropical species due to greater spatial distances between

current temperatures and their future analogs in the tropics than in temperate zones (Beaumont *et al.*, 2011; Wright *et al.*, 2009) and generally narrower climatic niches due to a higher degree of climatic stability (on daily, seasonal, interannual and longer-term timescales) and higher niche specialization (Deutsch *et al.*, 2008; Janzen, 1967; McCain, 2009; Sheldon *et al.*, 2011; Sunday *et al.*, 2011; Terborgh, 1973). As a result, tropical species are predicted to lose climatically suitable habitat faster and will have to migrate greater distances to keep within their suitable climates than will temperate species (Loarie *et al.*, 2009; Malcolm *et al.*, 2002; Wright *et al.*, 2009). Furthermore, for much of the moist lowland tropics, future climates will have no nearby analog (Williams *et al.*, 2007; Wright *et al.*, 2009), meaning that rate of local extinction may exceed colonization,

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resulting in net species loss (i.e., 'biotic attrition'; Colwell *et al.*, 2008; Feeley & Silman, 2010a).

Assuming that tropical species are able to track changes in the location of climatically suitable habitat, the shallow latitudinal temperature gradient found in the tropics (Sunday *et al.*, 2011; Terborgh, 1973) means that they are more likely to shift their ranges upslope rather than pole-ward. As land area tends to decrease at higher elevations, elevational range shifts may potentially result in reduced habitat areas and population sizes (Feeley & Silman, 2010b). Another factor which will decrease future habitat areas and population sizes is deforestation (Feeley & Silman, 2010b). In the case of Amazonia, which comprises approximately half of the total global tropical forest area, deforestation had already resulted in approximately 15% loss of forest cover by 2002, with most forest loss concentrated in the southern 'arc of deforestation' (Soares-Filho *et al.*, 2006). By 2050, the loss of habitat area is predicted to increase to 26% or 47% under simulated progressions of increased governance (GOV) or business-as-usual (BAU) deforestation, respectively (Soares-Filho *et al.*, 2006).

While climate change and deforestation are widely recognized as major threats to tropical diversity (Asner *et al.*, 2010; Brodie *et al.*, 2012; Corlett, 2011; Laurance & Wright, 2009; Malhi *et al.*, 2008; Peres *et al.*, 2010), few studies have made explicit predictions of their potential effects on tropical plants, and no study has quantitatively compared these effects. A major limitation has been the lack of information on current distributions because of the high number of species combined with the paucity of data available for most species (Feeley & Silman, 2011). For example, despite the high risk of climate-driven extinctions in the tropics, one widely publicized analysis of extinction risk due to climate change included only nine neotropical plant species (Thomas *et al.*, 2004), representing just 0.01% of estimated plant diversity for this region (Raven, 1988). Likewise, most predictions of species extinctions due to deforestation have used simulated species ranges or assumed panmictic distributions (Hubbell *et al.*, 2008; Pimm & Raven, 2000) and therefore have failed to account for spatial patterns or gradients in species distributions and disturbance (Feeley & Silman, 2008, 2009; Ter Steege *et al.*, 2003). Even for the few species for which spatially explicit range estimates have been used, predictions of future ranges may be confounded by the fact that current distributions are assumed to accurately reflect true climatic tolerances and no allowances have been made for changes in these tolerances through acclimation or adaptation and/or for truncated niches (Feeley & Silman, 2010a).

The recent integration of large numbers of tropical plant herbarium collection records into online databases such as the Global Biodiversity and Information Facility (www.gbif.org) and SpeciesLink (<http://splink.cria.org.br/>) has facilitated a several orders of magnitude expansion in the amount of information available for mapping tropical plant species' distributions (Fig. 1). We exploited these new compilations of georeferenced herbarium collections data to map the current distributions of 2779 Amazonian plant species on the basis of their known occurrence locations (Fig. 2; see Supplemental Information for a list of all contributing herbaria) in relation to mean annual temperature, drought intensity, and ecoregion (a proxy for other nonclimatic habitat variables such as soil; Feeley & Silman, 2009; Olson *et al.*, 2001). We then projected these distributions into the future under different future climate and land-use scenarios and asked: how will the distributions (area and location) of individual species and patterns of local diversity change due to climate change and/or deforestation?

Projections of species' ranges into the future were performed incorporating different assumptions regarding magnitudes of climate change and deforestation as well as species' responses to these changes. Specifically, we projected species ranges under all possible combinations of: (1) magnitude of global warming (global mean warming of +2 °C vs. +4 °C above pre-industrial levels); (2) change in plant water-use efficiency (WUE) due to rising concentrations of atmospheric CO₂ (improved WUE vs. unchanged WUE); (3) species migration ability within the bounds of their occupied

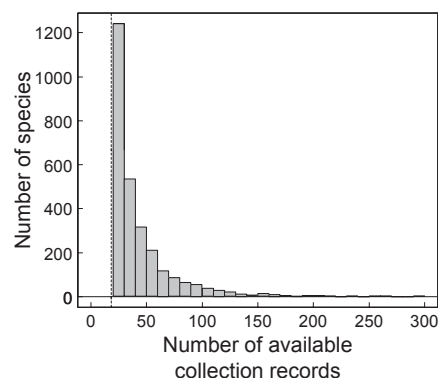


Fig. 1 Number of georeferenced collections per each of the 2779 Amazonian vascular plant species included in the study. The minimum number of collections per species was 20 (vertical dashed line) and the median number of collections per species was 33. Collections were downloaded through the Global Biodiversity Information Facility (GBIF: <http://www.gbif.org>) and SpeciesLink (<http://splink.cria.org.br/>) online data portals and screened for data quality and geo-referencing errors.

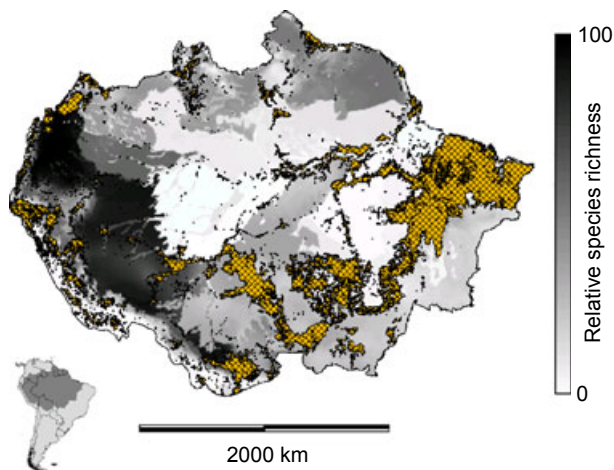


Fig. 2 Current relative richness of the 2779 study plant species in Amazonia as predicted from the overlapping species distribution models. Hatching indicates areas that were deforested as of 2002.

ecoregions (perfect vs. none); (4) ability of plant species to adapt to elevated temperatures and/or tolerate hotter temperatures due to niche truncation (limited vs. none); and (5) extent of deforestation (reduced [GOV] vs. business-as-usual [BAU]).

By modeling changes in species' distributions and diversity under these various scenarios we are able to generate best- and worst-case predictions as well as a range of intermediate predictions. Comparing the changes projected under these various assumptions also allows us to determine the relative importance and effects of uncertainty in each of the factors (e.g., rate of global warming vs. extent of deforestation) which will help to guide future research and conservation efforts.

Materials and methods

The contemporary (1960–1990) climate of tropical South America was characterized using the WorldClim climate database (Hijmans *et al.*, 2005) at a scale 2.5 arc-minute grid cells (approximately 5×5 km at equator). We extracted estimates of mean annual temperatures (hereafter referred to as temperature), and used extracted monthly precipitation estimates to calculate the Maximum Climatological Water Deficit (MCWD; Malhi *et al.*, 2009). The MCWD, which integrates magnitude and seasonality of precipitation to measure the degree of water stress that accumulates over the course of a dry season, has been found to be a strong predictor of the distribution of humid tropical forest and other biomes within the tropics (Malhi *et al.*, 2009; Zelazowski *et al.*, 2011). We calculated MCWD as the most negative value of climatological water deficit (CWD) over a year, where the monthly change in CWD is precipitation (P ; mm/month) – evapotranspiration (E ; mm/

month) such that for month i : $CWD_i = CWD_{i-1} + P_i - E_i$; $\text{Max}(CWD_i) = 0$; $CWD_0 = CWD_{12}$; $MCWD = -\text{Min}(CWD_1 \dots CWD_{12})$. In calculating MCWD, we assumed that the soil is saturated (i.e., CWD set to 0) at the wettest month of the year and we started the twelve-month calculation cycle from this point. We did not directly estimate E but rather used a fixed value of 100 mm/month that approximates an evapotranspiration rate for nondrought stressed humid tropical forests found in observational studies (Fisher *et al.*, 2009, 2011; Malhi *et al.*, 2002). Moderate variations in the assumed value of E have been found to have little effect on the spatial patterns of MCWD, and fixed values of E have been found to be as robust at predicting tropical forest distribution as more explicitly modeled values of E (Zelazowski *et al.*, 2011) (Supplemental Information, Fig. S1).

We downloaded all vascular plant herbarium collection records for tropical South America identified to species and including collection coordinates available through the Global Biodiversity Information Facility (GBIF: <http://www.gbif.org>) and SpeciesLink (<http://splink.cria.org.br>) online data portals (see Supporting Information for a list of herbaria contributing collections data to this study). We identified and removed duplicate records by screening for unique combinations of species name, latitude, and longitude (rounded to nearest 0.01° = approximately 1 km at the equator; rounding performed to catch duplicate records with geo-referencing data presented at different resolutions). We also applied several data filters to minimize geo-referencing errors, which can severely impact estimates of species distributions. Specifically, when downloading collection records we used the available automatic filters to eliminate records with obvious geo-referencing errors (in the case of GBIF, we filtered for records 'without known coordinate issues' and in SpeciesLink, we filtered for records whose coordinates were 'not suspect'). We also eliminated any records with collection coordinates falling over large bodies of water. In addition, we excluded all records for which the difference between the collection elevation as recorded with the herbarium metadata vs. as extracted at the collection location from a Shuttle Radar Topography Mission Digital Elevation Model (SRTM DEM; <http://www2.jpl.nasa.gov/srtm/>; ground scale of 30 arc-seconds and vertical accuracy of ca. ± 16 m) exceeds 100 m (Feeley & Silman, 2010c).

For each of the 2779 plant species with ≥ 20 specimens remaining after filtering (Fig. 1), we estimated the upper and lower limits of their thermal and drought tolerance niches as the 2.5% and 97.5% quantiles of the temperature and MCWD values, respectively, extracted at the collection coordinates. Quantiles were used rather than absolute minimum and maximum to reduce the impacts of outliers potentially caused by errors in species identification, geo-referencing, or digitizing. In addition, we also extracted the identity of all ecoregions (as defined by WWF; Olson *et al.*, 2001) for each collected species. Ecoregions were included to serve as a proxy for soil type and/or other nonclimatic factors that may limit the potential distributions of plant species. The potential biases and errors associated with using ecoregions to map species distributions

are discussed in Feeley & Silman (2009). We elected to use this relatively simple species distribution model (SDM), which is a modification of the popular BIOCLIM model based on rectilinear climate envelopes, rather than more sophisticated SDMs such as those based on machine learning or ensemble methods (Arajo & New, 2007; Phillips *et al.*, 2006; Thuiller, 2003), because of its greater flexibility which allows us to model the current and future distributions of large numbers of species under a variety of conditions and assumptions. In addition, the SDM of choice has low omission error and high commission error rates and tends to overestimate species ranges compared with other models since it considers the environmental variables independently and of equal weight. For example, in an analysis of 500 of our study species (randomly selected), we found that our estimates of current ranges were a median of 81% larger (95% CI = 68–102%) than range estimates created using the machine learning-based SDM, MAXENT (Phillips *et al.*, 2006), with comparable inputs and settings (Supplemental Information, Fig. S6). As the threat of climate change-induced extinction is generally elevated for small-ranged species (especially when species have no or limited migration ability as assumed in our model), our results are likely to be conservative.

We next quantified the area of suitable habitat currently available to each species as the number of pixels within the currently occupied ecoregions having temperature and MCWD values falling within the species' estimated thermal and drought tolerances. To limit the focus of our study to just the areas for which spatially explicit information on current and future deforestation rates is available, we only tallied suitable areas within Amazonia (note that species requirements were based on the climatic and ecoregion distributions of all available herbarium collection records including those from outside the Amazon). In estimating species' ranges and patterns of species diversity, we accounted for deforestation by overlaying a map of current (2002) deforestation (Soares-Filho *et al.*, 2006) and assuming a complete loss of natural plant species diversity in all of the deforested areas.

As a first-order approximation of future climate regime we modified the high-resolution contemporary climate data according to climate anomaly patterns (local and seasonal change in climate variable per degree of warming over land) at a spatial resolution of 2.5×3.75 arc-degree (Zelazowski *et al.*, 2011). The patterns were derived from the ensemble predictions of 17 Atmosphere-Ocean Global Climate Models (AOGCMs; data available at the WCRP CMIP3 portal; <https://esg.llnl.gov:8443>). To circumvent the problem of known biases in the description of the current climate by some AOGCMs, which is especially important in the case of tropical rainfall, each precipitation pattern was multiplied by the ratio of observed to modeled value. Subsequently, the patterns were scaled according to investigated climate scenarios (see below), re-sampled to higher resolution, smoothed with average filter, and added to the high-resolution climatology. This approach assumes that the sub-grid patterns and relative magnitudes of rainfall and temperature are preserved under a climate change pattern. The main advantage of this approach is in highlighting the existence of localized vulnerable or

resilient regions in greater detail, something impossible from a low-resolution analysis alone.

To estimate the effects of future climate and land-use change on suitable habitat areas and patterns of Amazonian diversity, we tallied the amount of land area (i.e., number of pixels) estimated to be suitable to each species under future conditions (i.e., areas within the species' currently occupied Amazonian ecoregions and with future climates estimated to fall within the species' thermal and drought tolerance niches).

In tallying the amount of suitable land area that will be available to species under future conditions, we used all possible combinations of several different assumptions regarding how tropical plant species will respond to rising temperatures and increasing concentrations of atmospheric CO₂, as well as different assumptions regarding future rates of Amazonian deforestation (Supplemental Information, Figs S4 & S5). Specifically:

1) *Mean global warming reaches 4 °C vs. mean global warming only reaches 2 °C*: Climate patterns (both in temperature and precipitation) were scaled to reflect the regime at either 2 or 4 °C mean global warming (above pre-industrial levels), according to the climate sensitivity of each AOGCM, and then averaged. This rescaling to degree global warming rather than a particular reference year is advantageous because it bypasses discussion of the merits or probability of particular emissions scenarios, it allows the depiction of extreme regimes (e.g., 4 degrees increase in global temperature) even if they were not reached in some of the original AOGCM simulations, and is more policy relevant in terms of international negotiation targets such as limiting global warming to <2 °C (Supplemental Information, Fig. S1). We elected to focus our analyses on just the mean ensemble climate predictions as analyzing results from all 17 climate models, which cover all possible moisture states (from large-scale dieback to models that make the whole Amazon wetter) would obscure patterns. For clarity, we emphasize that the 2 °C and 4 °C global warming scenarios used in the analyses incorporate changes in precipitation and MCWD patterns as well as changes in temperature.

2) *Rising concentrations of atmospheric CO₂ will not affect plant water-use efficiency (WUE)*: We tallied future suitable land area as above.

vs. Rising [CO₂] will result in improved WUE: We recalculated the maps depicting future MCWD accounting for increased plant WUE by decreasing mean evapotranspiration by 12.5 or 25 mm month⁻¹ when calculating MCWD under 2 °C and 4 °C global warming scenarios, respectively, (based on approximate estimates derived using the Met Office Surface Exchange Scheme; Cox *et al.*, 1998; Zelazowski *et al.*, 2011).

3) *Species are incapable of migrating or extending their ranges to include areas outside their current distributions*: We tallied only those areas that are deemed suitable under both current and predicted future conditions.

vs. Species are capable of perfect migration and can track the projected changes in suitable habitat area within occupied ecoregions: We tallied all areas within the currently occupied ecoregions that are deemed suitable under future climatic conditions regardless of overlap with the species' current

range. Species were not permitted to migrate from one ecoregion to another as this delineation was used as a proxy for soil type and other variables that will not necessarily change in concert with climate (Feeley & Silman, 2009). The use of ecoregions also prevents large jumps in distributions or discontinuities between current and future distributions. For example, by restricting migration to within ecoregions we prevent plant species specialized for infertile soils in eastern Amazonia from migrating onto fertile soils in western Amazonia or species currently growing exclusively in the Guyana highlands from migrating to the Andes. Such an assumption, although not perfect, is more realistic than assuming free migration regardless of distance across all soil and landform types.

4) *Species are incapable of adapting to increasing temperature:* We tallied the amount of land area (number of pixels) within the species' currently occupied ecoregions that are estimated to have temperature and MCWD values within the species' thermal and drought tolerance niches, respectively.

vs. Species have a limited ability to tolerate and/or adapt to elevated temperatures: We tallied areas within all occupied Amazonian ecoregions that will 1) have future climates falling within the species' current climatic niches plus 2) any areas that are currently occupied but that would otherwise be deemed too hot in the future if that area is predicted to have suitable MCWD values and will not be more than 10 °C hotter than the species' lower thermal niche limit. This effectively allows species to tolerate or adapt to future warming by expanding their thermal niches to include warmer temperatures but only up to a maximum niche breadth of 10 °C. 10 °C is the approximate mean thermal niche breadth previously estimated for Amazonian plant species in the absence of thermal niche truncation; i.e., for species whose thermal niche limits do not include the maximum or minimum temperatures for tropical South America (Feeley & Silman, 2010a) (Supplemental Information, Fig. S2). If a species' current thermal niche breadth is ≥ 10 °C, we used the current niche breadth but did not allow for expansion (Supplemental Information, Fig. S3). The issue of truncated niches does not arise for other environmental variables, such as MCWD, as the full possible environmental range of those variables is realized under current climate conditions.

5) *Extent of future deforestation is reduced due to increased governance vs. Future deforestation continues BAU:* We tallied all Amazonian areas deemed suitable and not estimated to be deforested under a map of future deforestation as predicted for 2050 under Soares-Filho *et al.*'s (2006) model assuming increased GOV or assuming deforestation continuing BAU. As the climate projections are time-independent, using deforestation projections for 2050 effectively assumes either that the changes in climate have occurred by 2050 or that the extent of deforestation does not increase beyond what is predicted for 2050.

In addition to estimating the amount and location of land area suitable to each species under future conditions, we also estimated future patterns of diversity, as well as changes in relative species richness across Amazonia by tallying the number of overlapping species ranges predicted for each pixel

under current conditions and under each of the possible future scenarios.

Results

Under our best-case scenarios (deforestation rates are decreased due to increased GOV, there is a positive effect of increasing [CO₂] on plant WUE, species migrate perfectly within currently occupied ecoregions, and species can adapt to rising temperatures; scenarios nos. 2 and 10 in Table 1), we predict that the amount of climatically suitable habitat available to many species will increase, thereby offsetting some of the areas that will be lost to these species due to deforestation. Specifically, with 2 °C mean global warming we predict that the study species will lose a median of just 8.2% (95% CI = 7.7–8.6%) of their current habitat area (accounting for areas already lost due to current deforestation; Table 1; Fig. 3a). If global warming increases to 4 °C (Fig. 3d), we predict a median habitat loss of 11.6% (10.4–12.7%). In both cases, the amount of habitat lost per species through the combined effects of climate change and deforestation is significantly less than the projected losses due to deforestation alone (the median habitat loss due to deforestation alone with increased GOV is 13.5%; Table 1) as species expand their ranges and/or shift their ranges to less disturbed areas. The median value of local diversity change predicted under this best-case scenario is a decrease of 4.1% (4.0–4.2%) in species richness with 2 °C global warming or a decrease of 25.0% (25.0–25.0%) in richness with 4 °C global warming (excluding areas already deforested as of 2002; Table 1; Fig. 4).

Under our worst-case scenarios (Scenarios nos. 26 and 34 in Table 1) in which we assume that deforestation follows a BAU trajectory, there is no effect of increasing [CO₂] on WUE, species are incapable of migrating, and that species are incapable of acclimating and/or adapting to rising temperatures, we predict that there will be massive decreases in the ranges of almost all species and associated losses of local diversity throughout Amazonia, with most areas experiencing a total or near total loss of diversity. Specifically, we predict that our study species will lose a median of 81.5% (80.6–82.7%) of their current habitat area under 2 °C global warming and 98.7% (98.5–98.9%) of their current habitat area with 4 °C global warming (Table 1; Fig. 3). Under this worst-case combination of assumptions, the median change in richness of the study species will be an 89.8% (89.1–90.5%) decrease with 2 °C warming. With 4 °C mean global warming, we predict that the median loss of local diversity of study species will increase to 100% (Table 1; Fig. 4).

Table 1 Percent loss of habitat area and percent change of diversity (median and 95% CI) predicted under various assumptions regarding the rate of deforestation, the magnitude of global climate change, and the responses of plant species

#	Assumptions					Predictions	
	Deforestation	Climate change	Species responses			Loss of habitat area median (95% CI)	Change in sp. richness median (95% CI)
			WUE ~ [CO ₂]	Migration	Thermal adaptation		
1	GOV	None	–	–	–	13.47 (13.36–13.64)	–
2			Yes	Yes	Yes	8.21 (7.69–8.59)	–4.14 (–4.03 to –4.23)
3					No	73.70 (72.31–74.86)	–74.66 (–74.15 to –75.00)
4		+2 °C		No	Yes	14.62 (14.39–14.87)	–8.03 (–7.99 to –8.07)
5					No	78.82 (77.46–79.74)	–75.00 (–75.00 to –75.00)
6			No	Yes	Yes	13.07 (12.85–13.33)	–7.95 (–7.89 to –8.02)
7					No	76.28 (74.95–77.38)	–75.00 (–74.64 to –75.00)
8				No	Yes	15.59 (15.37–15.80)	–8.70 (–8.62 to –8.74)
9					No	78.86 (77.64–79.87)	–75.00 (–75.00 to –75.00)
10			Yes	Yes	Yes	11.58 (10.41–12.7)	–25.00 (–25.00 to –25.00)
11					No	95.19 (94.94–95.34)	–100.00 (–100.00 to –100.00)
12				No	Yes	24.69 (22.45–27.13)	–30.99 (–30.86 to –31.14)
13					No	98.42 (98.23–98.58)	–100.00 (–100.00 to –100.00)
14			No	Yes	Yes	23.62 (22.55–25.02)	–34.70 (–34.48 to –34.96)
15					No	96.05 (95.91–96.22)	–100.00 (–100.00 to –100.00)
16				No	Yes	30.40 (28.81–31.96)	–35.95 (–35.68 to –36.13)
17					No	98.52 (98.32–98.71)	–100.00 (–100.00 to –100.00)
18	BAU	None	–	–	–	22.47 (22.17–22.92)	–
19			Yes	Yes	Yes	20.28 (19.84–20.77)	–6.29 (–6.20 to –6.40)
20					No	78.18 (76.82–79.30)	–89.05 (–88.44 to –89.64)
21		+4 °C		No	Yes	25.32 (24.58–25.93)	–10.12 (–10.03 to –10.21)
22					No	81.19 (80.31–82.39)	–89.66 (–89.14 to –90.20)
23			No	Yes	Yes	23.00 (22.48–23.52)	–10.70 (–10.53 to –10.84)
24					No	79.32 (78.10–80.30)	–89.61 (–89.00 to –90.41)
25				No	Yes	26.08 (25.55–26.59)	–11.28 (–11.13 to –11.43)
26					No	81.50 (80.55–82.67)	–89.75 (–89.14 to –90.45)
27			Yes	Yes	Yes	22.88 (21.73–24.03)	–28.37 (–28.11 to –28.67)
28					No	95.70 (95.49–95.87)	–100.00 (–100.00 to –100.00)
29				No	Yes	34.73 (33.57–36.13)	–35.60 (–35.37 to –35.82)
30					No	98.61 (98.45–98.77)	–100.00 (–100.00 to –100.00)
31			No	Yes	Yes	33.16 (32.39–34.29)	–42.16 (–41.77 to –42.50)
32					No	96.48 (96.31–96.62)	–100.00 (–100.00 to –100.00)
33				No	Yes	39.80 (38.24–41.20)	–43.14 (–42.76 to –43.34)
34					No	98.72 (98.55–98.88)	–100.00 (–100.00 to –100.00)

CI, confidence interval; GOV, governance; BAU, business-as-usual; WUE, water-use efficiency.

In addition to these best- and worst-case scenarios, we predicted the potential impacts of climate change and deforestation on the habitat areas of species and patterns of local diversity under a wide range of possible intermediate scenarios (Table 1). These intermediate scenarios provide insights into the relative magnitudes and effects of changing individual assumptions on the predicted changes in species habitat areas (Fig. 5). For example, we can examine the predictions under the assumptions that there is no effect of increased [CO₂] on WUE and that species are incapable of migrating but can adapt to rising temperatures (scenarios 8, 16 for

GOV and 25, 33 for BAU in Table 1; Figs 3b,e and 4b,e). This can be considered an exploration of the relative influence of deforestation and climate change-induced drought, in the absence of temperature or CO₂ effects. In this scenario, climate change effects on species loss are concentrated in the drying eastern Amazon region, where drought stress has increased. This is co-located with the area of strongest deforestation and forest fragmentation. In western Amazonia, the deforestation influence appears to dominate over any climate change influence. Under this set of assumptions and GOV deforestation, we predict that our study species will

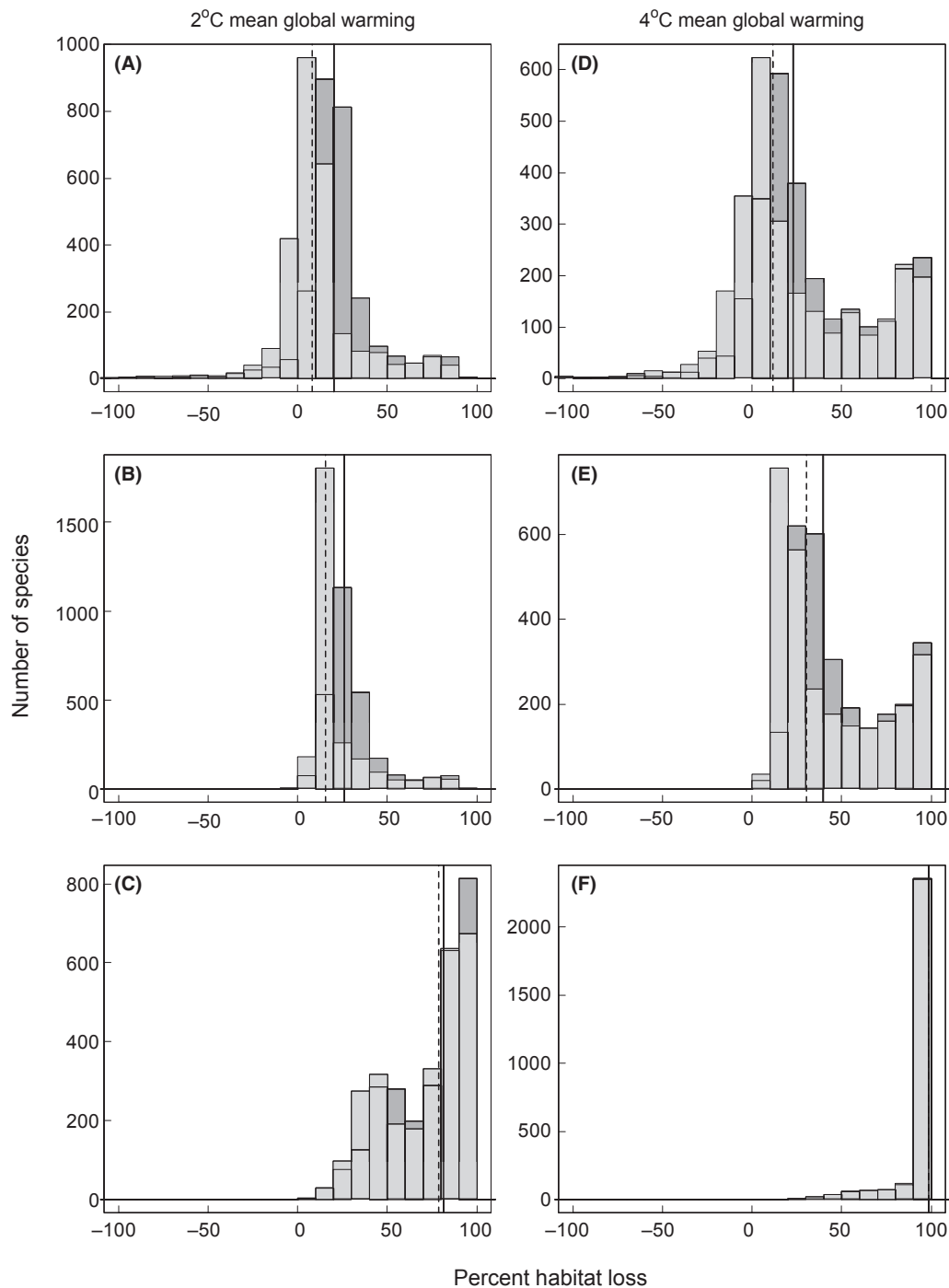


Fig. 3 Percent habitat loss relative to current habitat area (i.e., incorporating deforestation as of 2002; positive values indicate decrease in habitat area) predicted for each of 2779 Amazonian plant species under selected disturbance and species response scenarios. The top row of panels (A & D) shows predictions assuming increased water-use efficiency (WUE) under elevated CO_2 , species are capable of limited migration, and species are able to adapt to increased temperatures (i.e., the best-case scenario); the middle row (B & E) shows predictions assuming no increased WUE, no migration, but with thermal adaptation; the bottom row (D & F) shows predictions assuming no increased WUE, no migration, and no thermal adaptation (i.e., the worst-case scenario). The left column (A, B, & C) shows predictions under 2 °C mean global warming and the right column (D, E, & F) shows predictions under 4 °C mean global warming. Light gray histograms show predictions under the increased governance (GOV) deforestation scenario and the dark gray histograms show predictions under the business-as-usual (BAU) deforestation scenario. The vertical lines indicate the median percent habitat loss (dashed = GOV deforestation, solid = BAU deforestation).

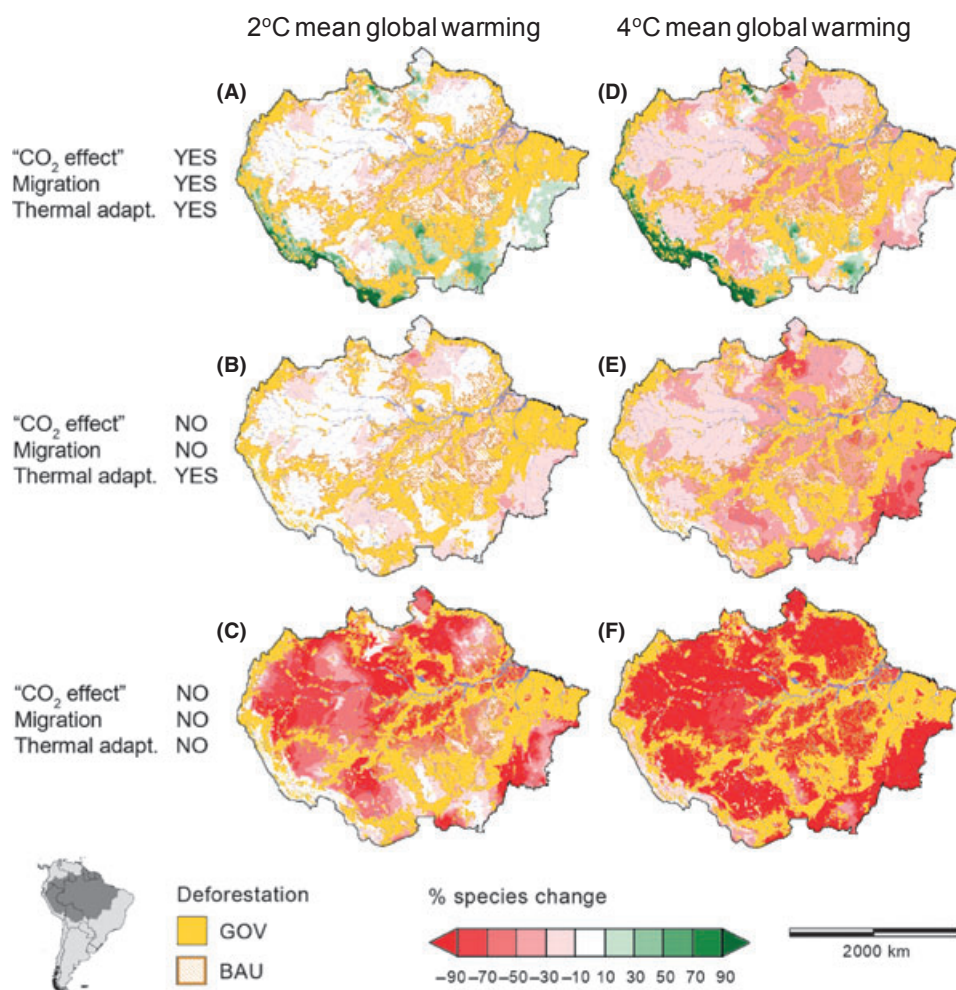


Fig. 4 Percent change in local plant species richness relative to current species richness as predicted from the species distribution models of the 2779 Amazonian study species under selected disturbance and species response scenarios (negative values indicate a decrease in species richness). The top row of panels (A & D) shows predictions assuming increased water-use efficiency (WUE) under elevated CO₂, species are capable of limited migration, and species are able to adapt to increased temperatures (i.e., the best-case scenario); the middle row (B & E) shows predictions assuming no increased WUE, no migration, but with thermal adaptation; the bottom row (D & F) shows predictions assuming no increased WUE, no migration, and no thermal adaptation (i.e., the worst-case scenario). The left column (A, B, & C) shows predictions under 2 °C mean global warming and the right column (D, E, & F) shows predictions under 4 °C mean global warming. Yellow filled and outlined areas show areas predicted to be deforested by 2050 under increased governance deforestation and business-as-usual deforestation scenarios, respectively.

lose a median of 15.6% (15.4–15.78%) of their current habitat area under 2 °C global warming and 26.1% (25.6–26.6%) of their current habitat area with 4 °C global warming; these values increase to 30.4% (28.8–32.0%) and 39.8% (38.2–41.2%), respectively, under BAU deforestation (Table 1; Fig. 3). The corresponding changes in the richness of the study species will be 8.7% (8.1–8.7%) and 11.3% (11.1–11.4%) decreases under GOV deforestation and 2 °C and 4 °C mean global warming, respectively; and 35.6% (35.7–36.1%) and 43.1% (42.8–43.3%) decreases with BAU deforestation and 2 °C and 4 °C mean global warming, respectively

(Table 1; Fig. 4). The results of other possible intermediate scenarios are presented in Table 1 and Fig. 5.

Discussion

In this study, we use a collated database of natural history collections combined with an ensemble GCM (rescaled to explore impacts under 2 °C and 4 °C global warming – a more policy-relevant approach than simulating to a fixed date when climate models differ in their climate sensitivity) to predict the effects of deforestation and/or climate change on the

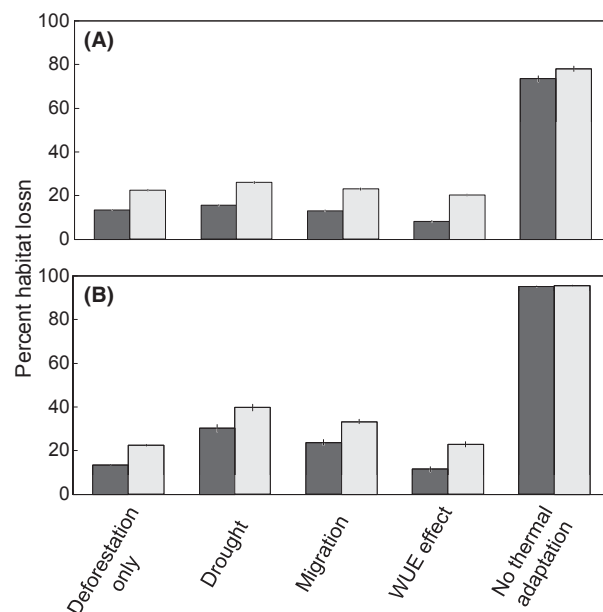


Fig. 5 The percent habitat loss predicted under various scenarios with (A) 2 °C mean global warming, and with (B) 4 °C mean global warming. Dark gray bars indicate predictions assuming increased governance and reduced deforestation; light gray bars indicate predictions assuming business-as-usual deforestation. Vertical lines indicate 95% confidence intervals. By incorporating a large number of assumptions into our analyses we are able to predict the potential impacts of climate change and deforestation on the habitat areas of species and patterns of local diversity under a wide range of possible scenarios (Table 1). In the main text we describe the predictions under our best and worst-case scenarios but we also explored various intermediate scenarios which provide insights into the relative magnitudes and effects of changing individual assumptions on the predicted changes in species' habitat areas. As an example, the figure shows the predicted effects that increased governance/reduced deforestation will have on changes in species habitat areas relative to the business-as-usual deforestation scenario in the absence of any climate change effects (scenarios 1 and 18 in Table 1), the additional effects of climate change-induced droughts (i.e., no water-use efficiency (WUE) effect, no migration, and limited thermal adaptation, scenarios 8, 16, 25, and 33 in Table 1), the relative importance of incorporating species migration (i.e., no WUE effect, limited migration, and limited thermal adaptation: scenarios 6, 14, 23, and 31 in Table 1), the relative importance of incorporating increased water-use efficiency due to elevated atmospheric concentrations of CO₂ (i.e., increased WUE, limited migration, and limited thermal adaptation: scenarios 2, 10, 19, and 27 in Table 1), and finally the effects of thermal adaptation (i.e., increased WUE, limited migration, and no thermal adaptation: scenarios 3, 11, 20, 28 in Table 1). Focusing on these sets of scenarios, we see that with increased governance and 2 °C mean global warming, climate change-induced changes in precipitation and water availability will have a relatively minor additional effect on species habitat areas beyond the losses already caused by deforestation (13.1 vs. 13.5% loss; Panel A). This is true even if species are unable to migrate and if there is no increase in water-use efficiency due to elevated CO₂ (15.6%). Indeed, the ability vs. inability of species to migrate has little predicted effects on the predicted changes of species habitat areas with 2 °C global warming. In contrast, incorporating increased WUE does have a significant effect such that the predicted degree of habitat loss when incorporating increased WUE (8.2%) is less than predicted due to deforestation alone. With 4 °C mean global warming (Panel B), the effects of changes in water availability are more pronounced, causing a near doubling (23.6 vs. 13.5 loss) in the magnitude of habitat loss when compared with the governance deforestation scenario alone. Likewise, allowing species migrations and incorporating increased WUE has magnified effects such that even with 4 °C warming, we predict that the loss of habitat area due to climate change and deforestation may still be less or equal to habitat losses due to deforestation alone (11.6% vs. 13.5 and 22.9 vs. 22.5 under governance and business-as-usual deforestation scenario, respectively; assuming thermal adaptation, see below). Overshadowing the effects of all other assumptions included in our analyses is the effect of thermal adaptation. If species are generally incapable of adapting to elevated temperatures, we predict a vastly elevated degree of habitat loss under both 2 °C and 4 °C global warming regardless of migration capability, changes in WUE, or rate of deforestation. In summary, in this single storyline an approximate ranking of the importance of factors with 4 °C mean global warming is (in declining importance): (1) ability of species to adapt to/tolerate rising temperatures, (2) changes in water availability, (3) changes in water-use efficiency, (4) rate of deforestation, and (5) ability of species to migrate. Also of note is that along this storyline the difference between the 2 °C and 4 °C global warming scenarios (Panel A vs. Panel B) is generally of similar magnitude to the difference between business-as-usual and governance scenarios of deforestation, which suggests that limiting the degree of global warming may be as important as slowing rates of deforestation in determining the future of Amazonian plant species.

distributions of several thousand Amazonian plant species and the consequent impacts on patterns of local biodiversity. We use a multi-factorial approach to explicitly and separately evaluate the relative importance of drought, temperature, CO₂-related changes in WUE, deforestation, and migration on species distributions under different climate and land-use change scenarios. In our worse-case scenarios, we predict that most species will face near-certain extinction due to extreme range contractions. On the other hand, more optimistic scenarios do exist in which we predict that changes in species' ranges will be greatly reduced and that many species may actually be able to expand their ranges (in some cases offsetting habitat loss due to deforestation). It is notable that the large differences between these best- and worst-case scenarios are due almost entirely to changing our assumptions about the ability of species to adapt to rising temperatures and/or tolerate a wider range of temperatures than predicted by their current distributions (Feeley & Silman, 2010a). In comparison, effects of [CO₂] on WUE, changes in species migration capability, and GOV vs. BAU deforestation, all had relatively little effect on habitat loss rates (Fig. 5; Supplemental Information, Figs S4 & S5).

These results help to highlight some of the key uncertainties in predicting the future of tropical biodiversity. If the thermal niches of many tropical species are approximated by current distributions (i.e., niches are not truncated) and remain fixed under warming rates on the order of 0.4 °C decade⁻¹ (Christensen *et al.*, 2007), there is a risk of substantial extinction and attrition of tropical lowland diversity over the next century. It should be emphasized here that the thermal niche reflects not just the physiological limits of the plant species, but the range of temperatures over which the plant species remains viable and competitive in the context of pollination, dispersion, herbivory, pathogen-load, and other ecosystem interactions. The potential effects of rising temperatures overshadow any effects of decreased water availability or even deforestation. Hence, the ability of tropical organisms to tolerate and/or adapt to warming is clearly one of the biggest sources of uncertainty governing the fate of tropical (and hence global) biodiversity. Tropical biodiversity appears to have remained high through previous warm periods (Jaramillo *et al.*, 2006), but the rates of tropical warming in previous rapid warming periods were about 100 times slower (e.g. ~5 °C over ~10 000–20 000 years; Zachos *et al.*, 2003) than those projected for the 21st century. It is unknown if the thermal niches of tropical species are broad enough or plastic enough to adapt to the much more rapid warming now underway.

Under all considered scenarios, except those assuming no migration, we predict that the Andes Mountains and Guyana highlands will increase in diversity and become important refugia as lowland species shift their distributions upslope to higher/colder areas in response to rising temperatures (Fig. 4). This result highlights the critical need for the conservation of forested landscapes in the Andes and other upland regions, as well as the migration routes connecting centers of lowland diversity to the future highland refugia (Brodie *et al.*, 2012; Killeen & Solórzano, 2008).

The presented predictions describe a range of possible outcomes of climate change and deforestation. Despite the range of permutations we have considered, our analysis still does not span the full range of potential outcomes. For clarity, we have focused only on the ensemble mean climate prediction across 17 climate models. The more 'pessimistic' individual climate models suggest strong drying and warming across Amazonia and thus a major influence of climate on species ranges, while in contrast the more 'optimistic' models suggest regional wetting and thus a negligible or even benign influence of climate change on species ranges (Malhi *et al.*, 2009). For deforestation, the recent remarkable reduction in habitat conversion rates in the Brazilian Amazon at least raises the prospect that total deforestation by 2050 could be even lower than predicted under the GOV scenario (Nepstad *et al.*, 2009). There are also other large-scale human disturbances which were not incorporated in our predictions, such as fire, logging and grazing (Feeley & Silman, 2010b; Nepstad *et al.*, 1999; Peres *et al.*, 2010), habitat fragmentation (Laurance *et al.*, 2002), or disruptions of biological interactions (Sheldon *et al.*, 2011) – all of which will greatly influence species distributions and patterns of future diversity (Brodie *et al.*, 2012). These disturbances will affect not only the amount of available habitat but also the responses of species to climate change and deforestation. Finally, we emphasize that the actual impacts of anthropogenic disturbances will be highly species-dependent as different Amazonian plant species exhibit different abilities to capitalize on changes in [CO₂] to improve WUE or photosynthetic rates, shift their distributions in response to changes in habitat suitability, tolerate or respond favorably to deforestation or other human land uses, and especially their ability to tolerate and/or adapt to rising temperatures. Thus while our results provide a general framework for predicting the possible effects of climate change and deforestation on Amazonian plant species distributions and patterns of diversity, a great deal of uncertainty remains to be resolved.

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Supporting Information

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

Table S1. List of herbaria contributing tropical plant collection records accessed through the Global Biodiversity Information Facility and SpeciesLink.

Figure S1. Maximum Climatological Water Deficit (MCWD; first row), and mean annual temperature (second row) coverages used in this study.

Figure S2. The observed thermal range, or niche breadth, of the 2779 study species vs. the upper (hot) limit to the estimated thermal niche.

Figure S3. Vertical bars indicating the thermal niches of each of the 2779 study species.

Figure S4. Percent habitat loss relative to current habitat area (i.e., incorporating deforestation as of 2002; positive values indicate decrease in habitat area) observed for each of 2779 Amazonian plant species under various combinations of assumptions.

Figure S5. Percent habitat loss relative to current habitat area (i.e., incorporating deforestation as of 2002; positive values indicate decrease in habitat area) observed for each of 2779 Amazonian plant species under the assumption that extant of future deforestation is based on business-as-usual rates (deforestation = 2050BAU) vs. extant of future deforestation is based on reduced rates due to increased governance (deforestation = 2050GOV).

Figure S6. Percent accordance (Kappa) vs. ratio of range areas for 500 randomly selected study species as predicted using the modified BIOCLIM species distribution model as used in the analyses vs. the range areas as predicted from the machine learning based MAXENT species distribution model.

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