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The impact of global climate change on tropical forest biodiversity in Amazonia

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ABSTRACT

Aim To model long-term trends in plant species distributions in response to predicted changes in global climate.

Location Amazonia.

Methods The impacts of expected global climate change on the potential and realized distributions of a representative sample of 69 individual Angiosperm species in Amazonia were simulated from 1990 to 2095. The climate trend followed the HADCM2GSa1 scenario, which assumes an annual 1% increase of atmospheric CO₂ content with effects mitigated by sulphate forcing. Potential distributions of species in one-degree grid cells were modelled using a suitability index and rectilinear envelope based on bioclimate variables. Realized distributions were additionally limited by spatial contiguity with, and proximity to, known record sites. A size-structured population model was simulated for each cell in the realized distributions to allow for lags in response to climate change, but dispersal was not included.

Results In the resulting simulations, 43% of all species became non-viable by 2095 because their potential distributions had changed drastically, but there was little change in the realized distributions of most species, owing to delays in population responses. Widely distributed species with high tolerance to environmental variation exhibited the least response to climate change, and species with narrow ranges and short generation times the greatest. Climate changed most in north-east Amazonia while the best remaining conditions for lowland moist forest species were in western Amazonia.

Main conclusions To maintain the greatest resilience of Amazonian biodiversity to climate change as modelled by HADCM2GSa1, highest priority should be given to strengthening and extending protected areas in western Amazonia that encompass lowland and montane forests.

Keywords

Amazonia, biodiversity mapping, biodiversity scenarios, biodiversity trends, climate change modelling, conservation planning, spatial interpolation, tropical forest.

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INTRODUCTION

Tropical moist forests in Amazonia are thought to contain at least 12% of all species of flowering plants in the world (Gentry, 1982), so there has been much speculation about the effects of impending global climate change on regional biodiversity (Hartshorn, 1992; Bawa & Markham, 1995). Initial modelling experiments, based on the outputs of general circulation models (GCMs) of climate change, have focused on the biome level. In simulations using six vegetation models forced by outputs from the Hadley Centre Second Generation Coupled Ocean-Atmosphere

GCM (HADCM2 Johns *et al.*, 1997), evergreen forest was succeeded by mixed forest, savanna and grassland in eastern Amazonia and savanna also expanded into parts of western Amazonia (Cramer *et al.*, 2001). In HADCM2-based simulations by White *et al.* (1999), savanna, grassland and even desert expanded into north-eastern Amazonia. More dramatically, simulations using the more recent HADCM3 showed forest loss over most of Amazonia (White *et al.*, 1999; Cox *et al.*, 2000), accelerated by positive feedback between warming and emissions of carbon from soil and vegetation. Until now, however, no modelling work has been carried out at the species level. This paper helps to fill this gap by

reporting the results of simulations of possible trends in the potential and realized distributions of a representative sample of Amazonian plant species in response to changes in climate forecast by a typical HADCM2 scenario for 1990–2095. Simulations of trends in potential distributions show changes in long-term viability, while modelling size-structured populations over each species' realized distribution gives a better impression of trends over time as it allows for lags in the response of species populations.

STUDY AREA

Amazonia, the hydrological basin of the River Amazon, is a largely lowland region, half surrounded by the Andes to the west and the Guiana Shield to the north. It covers approximately 6 million km² within the territories of Bolivia, Brazil, Colombia, Ecuador and Peru. The study used a 1° latitude-longitude grid for compatibility with Flora Neotropica monograph data. The set of grid cells falling entirely within the vector envelope constructed by the EOS Amazon Project (1998) is referred to as 'enclosed Amazonia'. This includes 426 × 1° cells, with a total area of 5.2 million km². Another 134 cells sit on the boundary of the envelope. The resulting total of 560 cells is called 'inclusive Amazonia'.

METHODS

Choice of general circulation model and scenarios

Of the various GCMs used to simulate alternative future scenarios for global climate, the UK Meteorological Office HADCM2 model (Johns *et al.*, 1997) was chosen for this study, as it performed better than other GCMs in simulating current precipitation in South America, and Amazonia in particular (Hulme *et al.*, 1999). HADCM2 simulations of future trends in temperature and precipitation in Amazonia are more consistent with those of other models than are those of the more recent HADCM3.

Two climate change scenarios were used in this study. The 'worst case', or Standard Impact (SI), scenario used bioclimatic variables derived from the IS92a 'business as usual' scenario of HADCM2. This is commonly used to represent the consequences of low levels of international action on climate change, and assumes a 1% compound annual increase in greenhouse gases from 1990 to 2099. The 'GSa' variant was chosen to include the effects of sulphate forcing, which to some extent mitigates greenhouse gas impacts (Mitchell *et al.*, 1995). Outputs for a single run, HADCM2GSa1, were used because mean outputs can lack internal consistency and obscure spatial patterns of change. The 'best case', or Reduced Impact (RI), scenario was derived from the SI scenario by arbitrarily resetting climate anomalies to exactly half of those simulated in it.

Species selection

Family selection

Stratification was used to select species for climate change impact assessment to ensure that the sample was as representative as

possible of taxonomic and functional biodiversity. Selection took place in four stages. First, a representative sample of families was identified. Some 132 families in the cladistic classification of the Angiosperm Phylogeny Group (APG) 1998 are known to occur in Amazonian lowland forest. Of these, 17 are endemic to the Neotropics. Using the APG cladogram, families were categorized as: (a) belonging to an informal group (clade) of orders in the cladistic classification; (b) belonging to an order outside these groups; or (c) lacking sufficient information to be assigned to any order. An ideal sample of families would include one from each group in category (a), one from each order in (b), and every family in (c). This rule was followed, with preference given to those families endemic to the Neotropics and having the most genera. [Proportionally more global biodiversity would be lost with the extinction of endemic families than of more cosmopolitan families. Families with many genera account for a high proportion of Amazonian flora and would be expected to hold a greater proportion of functional diversity if this was randomly distributed amongst genera]. More families were then added to each group to maximize representation of different life forms (see below).

Finally, to ensure comparability between the simulations for different species, the availability of distributional data for these selected families was evaluated, and families that had not been actively researched or the subject of monographs (Organization for Flora Neotropica, 1999) were eliminated. The selection procedure was then repeated for the clade to which each eliminated family belonged, and a replacement family was identified if possible. This led to the selection of 14 families: Arecaceae, Balanophoraceae, Bignoniaceae, Caryocaraceae, Chrysobalanaceae, Dioscoreaceae, Fabaceae, Lauraceae, Myrtaceae, Proteaceae, Rubiaceae, Triuridaceae, Sapotaceae and Zingiberaceae.

Species selection by spatial data availability

Second, species were selected from these families for which there were sufficient spatial data to construct a reasonable estimate of their distribution in 1990. A small number or low density of record points may indicate limited data, or simply that the distribution is very restricted — without a full survey, it is impossible to differentiate. Hence, species with ≤ 5 record-cells were excluded, as were species whose record-cell density within the recorded range fell below 0.35, unless the record-cell count exceeded an arbitrarily-defined upper limit of 50 (see Miles, 2002; for further details). Very narrow-range endemics were therefore excluded from this exercise; their distributions will frequently be limited by factors other than coarse-scale climate.

Distributional data published in monographs or in the scientific literature were supplemented by data provided by herbaria and family specialists. No species from the Dioscoreaceae, Myrtaceae, Triuridaceae or Zingiberaceae met our requirements. This resulted in a working set of 193 species.

Species selection by climate occupancy

Third, we aimed to ensure that the sample represented a range of adaptation to seasonality (and hence a range of responses to

possible changes in this dimension of climate). For each species, the mean seasonal moisture availability (mSMA, see below) was calculated for the set of record-cells. Up to three species from each family were then selected — those with the maximum, minimum and median mSMA. This established a subset from the working set.

Species selection by plant functional types

Fourth, the subset was expanded so it was a representative sample of plant functional types (PFTs), whose use was intended to maximize functional diversity as it related to climate change response. PFTs were defined by five traits that influence the processes determining a plant's response to climate change, namely reproductive rate, dispersal mechanisms and preadaptations to expected stresses. The traits were:

- 1 Life-form (annual herb, perennial herb, shrub, tree, epiphyte, climber (woody liana or herbaceous vine)).
- 2 Adult height class (< 1 m, 1–4 m, 4–10 m, 10–20 m, 20–25 m, and > 25 m).
- 3 Deciduousness (deciduous, semideciduous, deciduous under drought stress, evergreen).
- 4 Pollination mode (selfing, wind, vertebrate (flying), vertebrate (arboreal), invertebrate).
- 5 Dispersal mode (wind, vertebrate (flying), vertebrate (arboreal), vertebrate (swimming), water, vertebrate (ground), invertebrate, unassisted (explosive dehiscence, gravity, subterranean)).

All 193 species were grouped into PFTs having unique combinations of these traits as far as they could be determined (Clark & Clark, 1992; Erikson & Bremer, 1992; Gorchoff *et al.*, 1993; Listabarth, 1993; Condit *et al.*, 1995; Hammond & Brown, 1995; Ramírez, 1995; Gentry, 1996; Williams-Linera, 1997; Borchert, 1998; Bush & Rivera, 1998; Huante *et al.*, 1998; Killeen *et al.*, 1998; Küchmeister *et al.*, 1998; Brewer & Rejmánek, 1999; Gillespie, 1999; Ruiz & da Cruz Alencar, 1999; Roubik, 2000; van Roosmalen & da Cruz Gomes Garcia, 2000). The PFTs represented in each family were then tabulated, e.g. for the Fabaceae: (i) insect-pollinated, > 25 m, evergreen; (ii) insect-pollinated, 10–20 m, evergreen; (iii) insect-pollinated, 20–25 m, deciduous; (iv) insect-pollinated, 20–25 m, evergreen; (v) insect-pollinated, 1–4 m, evergreen. After species representing PFTs not already selected for each family had been added to the subset from the previous stage, this gave a final sample of 69 species (Table 1).

Spatial models of potential and realized species distributions

Constructing an initial map of the distribution of each species in 1990 from which to simulate future trends was not straightforward. Large-area biodiversity mapping in the humid tropics is severely constrained by: (a) a general lack of spatial data (even for these relatively well-known species), resulting from a paucity of extensive surveys; and (b) collection bias, as sample sites have been sited more for convenience than statistical rigour (Nelson *et al.*, 1990; Rose & Grainger, 2003). Spatial models were therefore produced of both potential and realized distributions.

A map of the *potential* distribution of each species in the 'extended Neotropics' (30° N to 30° S) was simulated using a suitability index (S_p), which estimates the suitability of an area for a given species in terms of prevailing environmental conditions. Where presence–absence data available, occurrence would be estimated instead as a probability, using a general linear model of the distribution based on bioclimate variables (e.g. Buckland & Elston, 1993). As this is not feasible with presence-only data, an alternative approach was taken, using a suitability index rather than a probability estimate. We chose three variables: actual evapotranspiration (AET); annual moisture deficit (MD), which is the difference between potential and actual evapotranspiration; and seasonality of moisture availability (SMA), which is the maximum number of consecutive days for which PET exceeds AET (the bioclimate model is detailed in Miles, 2002). First, a rectilinear envelope was defined, using for each species the maximum and minimum recorded values of the above bioclimatic variables, together with the minimum recorded temperature, in areas where it is found. Within these absolute constraints S_p was then calculated as the maximum similarity for each no-record location emerging from a comparison, using a Gower similarity metric (Gower, 1971; Carpenter *et al.*, 1993), of the values of each bioclimatic variable for each combination of record and no-record locations. S_p has a maximum value of 1 and a species is assumed to be viable in every cell where it exceeds a minimum value S_{min} . This value was defined on a species basis by finding the minimum positive value for record locations of a jack-knifed distribution of S_p (Crowley, 1992; Manly, 1992). Cells within the envelope and with $S_p > S_{min}$ were allocated to that species' potential distribution. However, species rarely, if ever, extend to their potential distributions, because of: (a) a limited ability to tolerate fluctuations in environmental conditions; and (b) the presence of dispersal barriers, such as mountains or farmland. In an attempt to simulate this, a map of the *realized* distribution of each species was produced that was limited to groups of grid cells within the potential distribution and contiguous with the species record. A spatial buffer was then used to limit the species' range, such that presences were only simulated within a distance less than or equal to the greatest distance between two species records. A 5° limit was used to avoid large buffers resulting from spatial outliers and overestimation of the range relative to more clustered species. However, it was not possible at this scale to allow for features that diminish but do not prevent dispersal, such as rivers or locally steep gradients.

Spatial equilibrium model of initial species distributions

A size-structured population was then simulated for every 1° grid cell in the realized distribution in inclusive Amazonia of each species in 1990. The detailed data required for an accurate simulation even of present-day populations are not available for Amazonian species, and will not be in the foreseeable future. The following approach (Fig. 1) uses available data to give a 'best guess' at a demographic response to change. The population was assumed to be in equilibrium with its environment, and dividing it into size classes (a seed class and up to six plant stages) allowed

Table 1 Changes in the viability of the representative set of species in 2095 in the SI and RI scenarios

Species	Family	Form	Height class (m)	% Cells Lost		% Cells Non-viable	
				scenario		scenario	
				SI	RI	SI	RI
<i>Amphilophium paniculatum</i> (L.) H.B.K.	Bignoniaceae	Liana	10–20	0.0	0.0	52.2	20.2
<i>Aniba panurensis</i> (Meissn.) Mez	Lauraceae	Tree	10–20	0.2	0.2	97.9	43.8
<i>Anthodiscus obovatus</i> , Benth. ex Wittm.	Caryocaraceae	Tree	20–25	0.0	0.0	100.0	100.0
<i>Arrabidaea corallina</i> (Jacq.) Sandwith	Bignoniaceae	Liana	> 25	0.0	0.0	74.7	21.3
<i>Astrocaryum gynacanthum</i> , Mart.	Arecaceae	Tree	4–10	0.0	0.0	100.0	60.7
<i>Astrocaryum murumuru</i> , Mart.	Arecaceae	Tree	10–20	0.0	0.0	93.7	41.0
<i>Astrocaryum sciophilum</i> (Miq.) Pulle	Arecaceae	Bush	1–4	0.0	0.0	100.0	100.0
<i>Bactris acanthocarpa</i> (Mart.) emend. Henderson	Arecaceae	Herb	0–1	0.0	0.0	100.0	63.4
<i>Callichlamys latifolia</i> (Rich.) K. Schum.	Bignoniaceae	Liana	20–25	0.0	0.0	58.6	7.5
<i>Caryocar brasiliense</i> , Cambess	Caryocaraceae	Tree	4–10	0.0	0.0	98.9	23.9
<i>Caryocar glabrum</i> (Aubl.) Pers.	Caryocaraceae	Tree	> 25	1.7	2.5	98.3	66.3
<i>Caryocar microcarpum</i> , A. Ducke	Caryocaraceae	Tree	20–25	0.0	0.0	100.0	54.8
<i>Chamaedorea fragrans</i> (Ruiz & Pav.) Mart.	Arecaceae	Bush	1–4	0.0	0.0	66.7	66.7
<i>Chrysobalanus icaco</i> , L.	Chrysobalanaceae	Bush	1–4	0.0	0.0	71.1	11.4
<i>Clytostoma binatum</i> (Thunb.) Sandwith	Bignoniaceae	Liana	20–25	0.0	0.0	43.0	1.9
<i>Couepia dolichopoda</i> , G.T. Prance	Chrysobalanaceae	Tree	> 25	0.0	0.0	100.0	59.4
<i>Couepia guianensis</i> , Aubl.	Chrysobalanaceae	Tree	> 25	0.0	0.0	100.0	79.2
<i>Couepia paraensis</i> , G.T. Prance	Chrysobalanaceae	Tree	10–20	0.0	0.0	100.0	30.9
<i>Cydista aequinoctalis</i> (L.) Miers	Bignoniaceae	Liana	4–10	2.4	2.5	52.2	7.5
<i>Geonoma macrostachys</i> , Mart.	Arecaceae	Bush	1–4	0.0	0.0	94.6	62.7
<i>Geonoma oldemanii</i> , Granv.	Arecaceae	Bush	1–4	0.0	0.0	100.0	100.0
<i>Gleasonia duidana</i> , Standl.	Rubiaceae	Tree	4–10	0.0	0.0	100.0	100.0
<i>Gleasonia uaupensis</i> , Ducke	Rubiaceae	Tree	4–10	0.0	0.0	100.0	100.0
<i>Helosis cayennensis</i> (Sw.) Spr.	Balanophoraceae	Herb	0–1	0.0	0.0	95.2	50.1
<i>Henriquezia nitida</i> , Spruce ex Benth.	Rubiaceae	Tree	10–20	0.0	0.0	100.0	100.0
<i>Henriquezia verticillata</i> , Spruce ex Benth.	Rubiaceae	Tree	> 25	0.0	0.0	100.0	94.4
<i>Hirtella ciliata</i> , Mart. & Zucc.	Chrysobalanaceae	Tree	4–10	0.0	0.0	81.4	6.8
<i>Hirtella glandulosa</i> , Spreng.	Chrysobalanaceae	Tree	20–25	0.0	0.0	66.0	22.7
<i>Hirtella gracilipes</i> (Hook. f) Prance	Chrysobalanaceae	Tree	10–20	0.0	0.0	80.9	24.3
<i>Hirtella mutisii</i> , E.P. Killip and J. Cuatrecasas	Chrysobalanaceae	Tree	> 25	0.0	0.0	100.0	100.0
<i>Hirtella paniculata</i> , Sw.	Chrysobalanaceae	Tree	4–10	0.0	0.0	100.0	69.7
<i>Hirtella triandra</i> , Sw.	Chrysobalanaceae	Tree	> 25	0.0	0.0	92.4	19.9
<i>Inga alba</i> (Swartz) Willdenow	Fabaceae	Tree	> 25	0.0	0.0	99.5	57.5
<i>Inga cardozana</i> , Sagot ex Benth.	Fabaceae	Tree	20–25	0.0	0.0	98.1	58.6
<i>Inga cayennensis</i> , L. Cárdenas	Fabaceae	Tree	20–25	0.0	0.0	100.0	75.0
<i>Inga ingoides</i> (Rich.) Willd.	Fabaceae	Tree	> 25	0.0	0.0	93.5	27.6
<i>Inga laurina</i> (Sw.) Willd.	Fabaceae	Tree	20–25	0.0	0.0	54.1	20.9
<i>Inga marginata</i> , Willd.	Fabaceae	Tree	20–25	0.2	0.4	89.5	24.3
<i>Inga nobilis</i> , Willd.	Fabaceae	Tree	10–20	0.0	0.2	71.2	3.9
<i>Inga plumifera</i> , Spruce ex Benth.	Fabaceae	Tree	4–10	0.0	0.0	100.0	100.0
<i>Iriartea deltoidea</i> , Ruiz & Pav.	Arecaceae	Tree	> 25	0.0	0.0	75.9	15.6
<i>Jacaranda macrocarpa</i> , Bureau & K. Schum. ex.Schum	Bignoniaceae	Tree	10–20	0.0	0.0	100.0	100.0
<i>Langsdorffia hypogaea</i> , Mart.	Balanophoraceae	Herb	0–1	0.0	0.0	76.6	20.2
<i>Leopoldinia major</i> , Wallace	Arecaceae	Tree	4–10	0.0	0.0	100.0	100.0
<i>Leopoldinia piassaba</i> , Wallace	Arecaceae	Tree	4–10	0.0	0.0	100.0	100.0
<i>Licania arborea</i> , Seem.	Chrysobalanaceae	Tree	> 25	0.0	0.0	95.3	75.7
<i>Licania heteromorpha</i> , G. Bentham	Chrysobalanaceae	Tree	20–25	0.0	0.0	98.8	69.2
<i>Licania humilis</i> , Cham. et Schldl.	Chrysobalanaceae	Bush	1–4	0.0	0.0	100.0	64.2
<i>Manilkara bidentata</i> (A.DC.) A. Chev.	Sapotaceae	Tree	> 25	0.0	0.0	85.2	63.8
<i>Martinella obovata</i> (Kunth) Bureau & K. Schum.	Bignoniaceae	Liana	1–4	0.0	0.0	94.0	51.5
<i>Nectandra amazonum</i> , Nees	Lauraceae	Tree	20–25	0.0	0.0	100.0	88.8
<i>Nectandra egensis</i> , Rohwer	Lauraceae	Tree	10–20	1.7	0.0	98.3	100.0

Table 1 continued

Species	Family	Form	Height class (m)	% Cells Lost		% Cells Non-viable	
				scenario		scenario	
				SI	RI	SI	RI
<i>Nectandra hihua</i> (Ruiz & Pav.) Rohwer	Lauraceae	Tree	> 25	0.0	0.0	85.7	23.5
<i>Nectandra reflexa</i> , Rohwer	Lauraceae	Tree	> 25	0.0	0.0	86.7	71.4
<i>Nectandra turbacensis</i> (Humboldt, Bonpland & Kunth) Nees	Lauraceae	Tree	20–25	0.0	0.0	92.7	39.7
<i>Oenocarpus bataua</i> , Mart.	Arecaceae	Tree	10–20	0.0	0.0	77.0	15.5
<i>Panopsis metcalftii</i> , Killip & Cuatrec.	Proteaceae	Tree	10–20	0.0	0.0	100.0	100.0
<i>Panopsis rubescens</i> (Pohl) Rusby	Proteaceae	Tree	> 25	0.0	0.0	100.0	50.7
<i>Parinari campestris</i> , Aubl.	Chrysobalanaceae	Tree	10–20	0.0	0.0	100.0	76.1
<i>Platycarpum schultesii</i> , Steyerl.	Rubiaceae	Tree	4–10	0.0	0.0	100.0	100.0
<i>Pouteria elegans</i> (A.DC.) Baehni	Sapotaceae	Tree	10–20	0.0	0.0	100.0	72.8
<i>Pouteria guianensis</i> , Aublet	Sapotaceae	Tree	> 25	0.0	0.0	83.3	61.3
<i>Pouteria reticulata</i> (Engler) Eyma	Sapotaceae	Tree	> 25	0.0	0.0	98.0	60.3
<i>Roupala montana</i> , Aubl.	Proteaceae	Tree	20–25	0.0	0.0	55.8	21.2
<i>Sarcaulus brasiliensis</i> (A.DC.) Eyma	Sapotaceae	Tree	20–25	0.0	0.0	98.9	71.6
<i>Socratea exorrhiza</i> (Mart.) H. Wendl.	Arecaceae	Tree	20–25	0.0	0.0	82.6	45.3
<i>Tabebuia nodosa</i> (Griseb.) Griseb.	Bignoniaceae	Tree	4–10	0.0	0.0	71.4	55.6
<i>Tabebuia serratifolia</i> (Vahl) G. Nicholson	Bignoniaceae	Tree	> 25	0.0	0.0	57.9	16.9
<i>Tecoma tenuiflora</i> (A. DC.) Fabris	Bignoniaceae	Bush	1–4	0.0	0.0	100.0	66.7

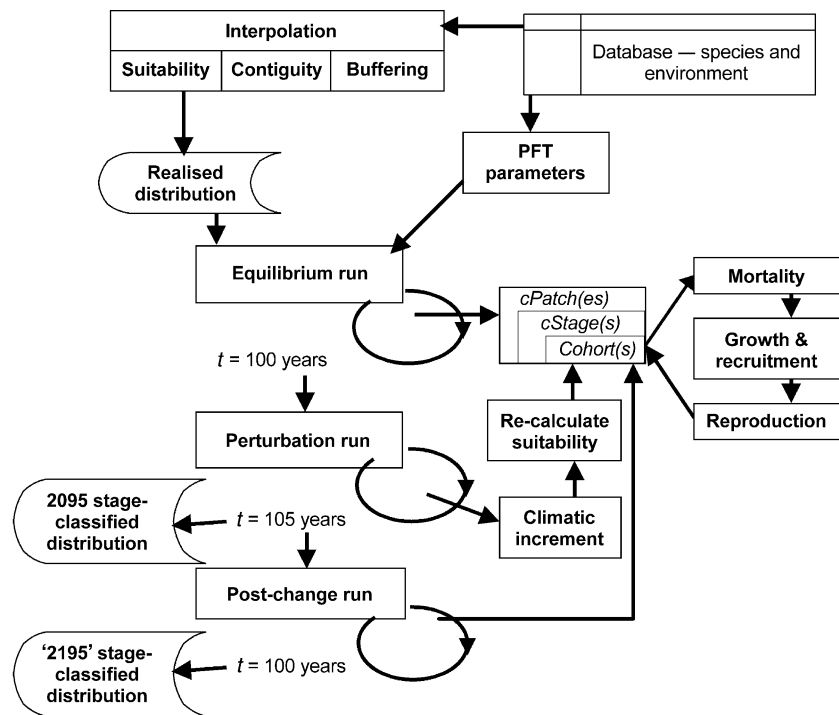


Figure 1 Model processes through simulated time.

lags in its response to climate change to be modelled. Each stage was populated by a number of cohorts, whose key attributes were germination year, population count and proportion of growth achieved towards the next stage (g). Other attributes, including the vital rates of survival, growth and reproduction, were shared between all cohorts in a stage. Cohorts moved between stages when $g = 1$ and there was space in the subsequent stage.

The size of a species population in a particular cell was expressed as a function of the balance between survival, growth and reproduction. Each stage (c) had a density limit, $K_{c\text{pmax}}$, which depended on environmental conditions. $K_{c\text{pmax}}$ was constrained by the available land area within that cell, and by the observed maximum density ($K_{c\text{max}}$), assumed constant for the particular stage and species. For stage c at the end of year y_1 ,

the number of individuals N_{cy1} was determined by the vital rates operating on the population remaining at the end of year y_0 , i.e.

$$N_{cy1} = \text{Recruits (reproduction}_{y1} \text{ or germination}_{c-1y1} \\ \text{or growth}_{c-1y1}) + \text{Survivors (survival}_{y1} * N_{cy0}) \\ - \text{Transition (growth}_{cy1} * \text{survival}_{y1} * N_{cy0})$$

This was translated into a population matrix equation encompassing all stages. The vector $n(t+1) = A_n(t)$ gave the number of individuals encountered in each stage for the interval t , with no temporal lag between stages. A single transfer matrix was used to describe the stage-specific rates of survival, reproduction and growth for all populations of a species. The coefficients of A for a cell p depended on climate and population density (K_{cp}) and could vary annually. The values of vital rate parameters were based on empirical data, with a simple set of rules limiting reproduction. Growth and survival relationships with the traits used to define the PFTs had been previously assessed using a tree and liana diameter dataset from permanent sample plots (Phillips *et al.*, 1998; Malhi *et al.*, 2002; Phillips *et al.*, 2002). Vital rates for a given species were used if they could be estimated using these or other data (Appendix 5 of Miles, 2002). Otherwise the PFT mean rate was used. Climate was represented by the three bioclimatic variables, AET, MD and SMA, plus the lowest mean monthly temperature T_{\min} .

It was assumed that every species had become adapted to a set of optimal conditions, surrounded by a band of tolerance within which vital rates were high enough to maintain a viable population. Exact relationships between population density and environmental variables for most tropical species cannot be inferred from the literature. So a 'most limiting factor' (MLF) approach was used, based on notional relationships (Shao & Halpin, 1995; Rutherford *et al.*, 1996; Hackett & Vanclay, 1998). A Gaussian response to each bioclimatic variable was assumed for K_{cpmax} , based on the three decadal mean values of the variables simulated for 1961–90 for the species presence records. The response surface optimum and tolerance were approximated using the mean value and standard deviation of the variable for presence sites (ter Braak & Prentice, 1988). The MLF was used to limit K_{cpmax} , and hence recruitment, at each location and point in time. The constraint on K_{cpmax} via recruitment limitation acted as a surrogate for the level of adversity presented by the climate, the density of individuals in a cell reflecting the climate's closeness to the physiological optimum for that species.

In each year, survival, germination, growth, recruitment, and reproduction were modelled in that order for each cohort. Stage-specific survival rates were applied to each cohort prior to recruitment to a given stage. If sufficient recruits were continuously available then K_{cp} would be maintained at K_{cpmax} . Each seed had an equal probability of germination and no limitation was applied to seedling numbers. If $S_p < S_{\min}$, germination was prevented on the grounds that the seed or seedling stage is the one most vulnerable to environmental conditions differing from those which the species currently inhabits. Recruitment was allowed when a cohort's growth was complete and the recipient stage was below maximum density, K_{cpmax} . Reproduction was calculated last, so that individuals recruited to a reproductive stage in

that year participated. The level of reproductive success for a cohort was assumed to depend on the probability of pollination, estimated using the density, stage and sex ratio of mature conspecifics.

The 1990 equilibrium population for each species in each cell was estimated by simulating the processes of germination, survival, growth, recruitment and reproduction for one hundred years under a stable climate, based on the mean 1961–91 climate of New *et al.* (1999).

Simulating responses of initial species distributions to climate change

The response of each species to future changes in climate will depend on how these affect its rates of survival, growth and reproduction. Ideally, this would have been modelled by simulating the relationship between each vital rate and an appropriate combination of climate variables. But as there were no reliable data with which to estimate such relationships, an alternative approach was adopted that limited recruitment according to the estimated equilibrium population density corresponding to the conditions in each simulated year. As climate changes, some cells will enter the habitable niche and create new areas of potential distribution. Other cells will leave the niche when $S_p < S_{\min}$ and their population will change status from viable to non-viable (relicts). Since established plants may tolerate suboptimal conditions, a non-viable population on an extinction trajectory may survive for a long time.

Just as for the equilibrium model, K_{cpmax} in any year was assumed to depend on the level of the MLF for each cell; recruitment was only permitted until that population density was achieved; and germination depended on the suitability index S_p . A population would therefore decline if S_p decreased, and be committed to extinction if: (a) the density of reproductive individuals was so low that obligate cross pollination was prevented; (b) there was no germination. However, there would be lags in population response. An increase in the limiting factor would increase K_{cpmax} , but recruitment to c would not happen until individuals in $c-1$ had grown to the maximum size for that stage. A decrease in the limiting factor would decrease K_{cpmax} , but this lower potential population density would not be achieved until mortality had removed sufficient individuals from the stage. The changing balance between mortality and recruitment therefore determines the success of a population within any one cell over time. Rates of growth, mortality and reproduction were conservatively assumed not to vary with climate, thereby lengthening the time taken for populations to be lost from the realized distribution.

Population processes were simulated annually from 1990 to 2095, based on changes in the bioclimatic variables simulated in the SI and RI scenarios. AET, PET and MD were calculated on a daily basis from interpolated decadal values of the GCM anomalies, without a stochastic element. The model was then simulated for a further 100 years under 2095 conditions to assess the surviving population's long-term viability.

The model depended on various assumptions, which are simplifications rather than assertions of reality. (i) Each species behaved independently of all others, such that interactions between

populations of a species could be disregarded at the 1° spatial scale; (ii) All populations of a species had the same environmental tolerances; (iii) Population processes could be simulated at this scale without obscuring any large area impacts of finer scale ecological patterns and events; (iv) Species occupying a similar environmental and functional niche had a similar response to climate change; (v) Individuals were distributed evenly within a cell; (vi) Species had recovered from or been unaffected by human influences, such as deforestation or logging; (vii) Evolutionary change operated too slowly to alter species traits over the simulation period and under the rate of environmental change considered; (viii) Sea-level rise did not reduce available land area; (ix) There were no net effects on plant life cycles from the elevated concentrations of greenhouse gases assumed in the IS92a scenario.

Implementing the model

The model was coded in Microsoft Visual Basic 6.0 as an object-orientated framework. Plant and climate data were accessed from and stored in a Microsoft Access 97 database. Various spatial functions were accessed through the Applications Programming Interface for IDRISI for Windows 2.0 (Eastman, 1997). The model was run for each species separately.

RESULTS

Simulated changes in climate between 1990 and 2095 showed actual evapotranspiration (AET) increasing in the west of Amazonia and decreasing in the north-east. The greatest rise in moisture deficit (MD) was in north-east Amazonia, and areas of high MD encroached into central Amazonia (Fig. 2). North-west Amazonia retained a relatively low MD throughout the period. Seasonality of moisture availability (SMA) was highest in the east, and by 2095 the north-east had a moisture deficit all through the year. SMA increased in most of Amazonia, indicating rising moisture stress, even in aseasonal forests, but it remained consistently low in the north-west.

Table 2 Species suggested by the SI and RI simulations to be under most threat from climate change, excluding those most likely to tolerate increased AET

Endemic to Amazonia	Not endemic to Amazonia
SI and RI Scenarios	SI and RI Scenarios
<i>Gleasonia uaupensis</i> , Ducke	<i>Anthodiscus obovatus</i>
<i>Inga plumifera</i> , Spruce ex Benth.	<i>Astrocaryum sciophilum</i> (Miq.) Pulle
<i>Jacaranda macrocarpa</i> , Bureau & K. Schum. ex. Schum	<i>Geonoma oldemanii</i> , Granv.
	<i>Gleasonia duidana</i> , Standl.
	<i>Henriquezia nitida</i> , Spruce ex Benth.
	<i>Hirtella mutisii</i> , E.P. Killip and J. Cuatrecasas
SI Scenarios only	SI Scenarios only
<i>Couepia dolichopoda</i> , G.T. Prance	<i>Astrocaryum gynacanthum</i> , Mart.
<i>Henriquezia verticillata</i> , Spruce ex Benth	<i>Inga cardozana</i> , Sagot ex Benth.
<i>Leopoldinia piassaba</i> , Wallace	<i>Leopoldinia major</i> , Wallace
<i>Nectandra egensis</i> , Rohwer	<i>Licania humilis</i> , Cham. et Schldl.
	<i>Nectandra amazonum</i> , Nees
	<i>Panopsis metcalfei</i> , Killip & Cuatrec.
	<i>Platycarpum schultesii</i> , Steyererm.

For most species no significant changes were simulated in their realized distributions between 1990 and 2095. No species became extinct over more than one third of its estimated range, although many populations declined to a very low density, which would render them vulnerable to extinction through stochastic external events and genetic drift.

On the other hand, there were significant changes in the potential distributions of all species, leaving many populations as non-viable relicts for which $S_p < S_{min}$ (Table 1). Populations became nonviable for 28 of the 69 species in the SI scenario, including *Astrocaryum gynacanthum* (Mart.), *Bactris acanthocarpa* ((Mart.) emend. Henderson), *Caryocar glabrum* ((Aubl.) Pers.), *C. microcarpum* (A. Ducke), *Couepia guianensis* (Aubl.), *C. paraensis* (G.T. Prance), and *Panopsis rubescens* ((Pohl) Rusby), and for 14 species in the RI scenario. The different trends in realized and potential distributions arose from the demographic lag in each population's response to climate change.

By 2095, 20 species in the SI scenario and nine species in the RI scenario either had no potential distribution at all, or their original distribution was situated so far from the new potential distribution that there was no realistic chance of reaching it by dispersal. Seven of these 20 species at most risk in the SI scenario are endemic to Amazonia and so would become extinct if these populations were lost (Table 2). The remainder of the species listed in Table 1 as having no viable populations by 2095 do have areas of potential distribution adjacent to their current realized distribution. It is therefore possible that under this scenario the species would be able to disperse into the newly suitable cells. The family with the largest mean percentage of each species' populations (30%) that retained viability was the Bignoniaceae. This mainly comprised tree and liana species occurring in a large number of cells, although the tree *Tabebuia nodosa* ((Griseb.) Griseb) with seven cells, found at the southern edge of Amazonia, did substantially better than the liana *Martinella obovata* ((Kunth) Bureau & K. Schum.) with 446 cells. The one shrub that was modelled in this family, *Tecoma tenuiflora* ((A. DC.) Fabris), lost viability throughout its small range. In contrast, all populations of all species of the Rubiaceae

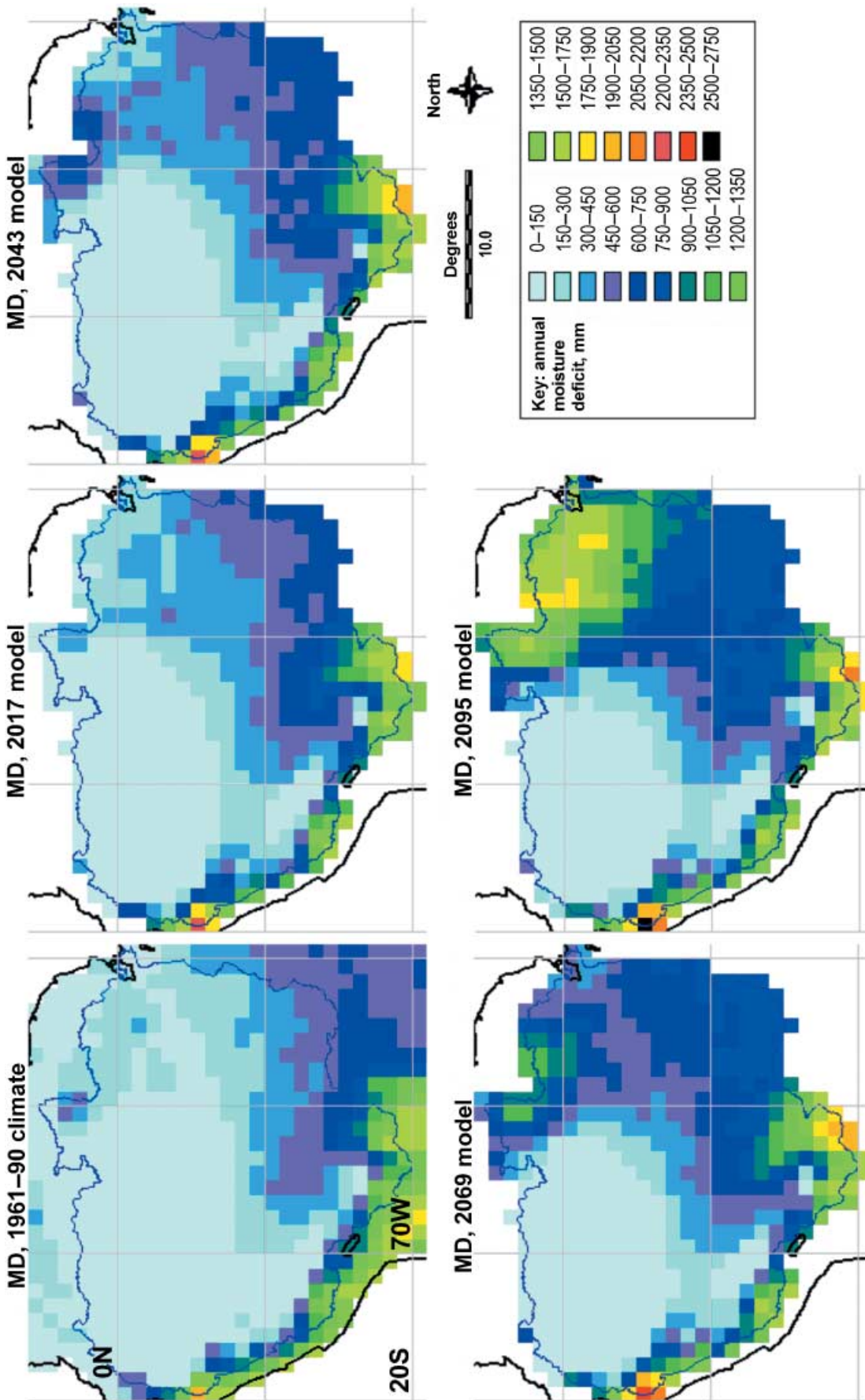


Figure 2 Changes in the distribution of moisture deficit (MD) in Amazonia 1990–2095 under the SI scenario. MD = PET – AET; modelled on a daily basis, based on variables downloaded from HADCM2GSa1 outputs. Major assumptions include: (i) that parameters related to vegetation type remained stable through the model run; (ii) that a simple linear scaling through time and space would be sufficient to model climate variation.

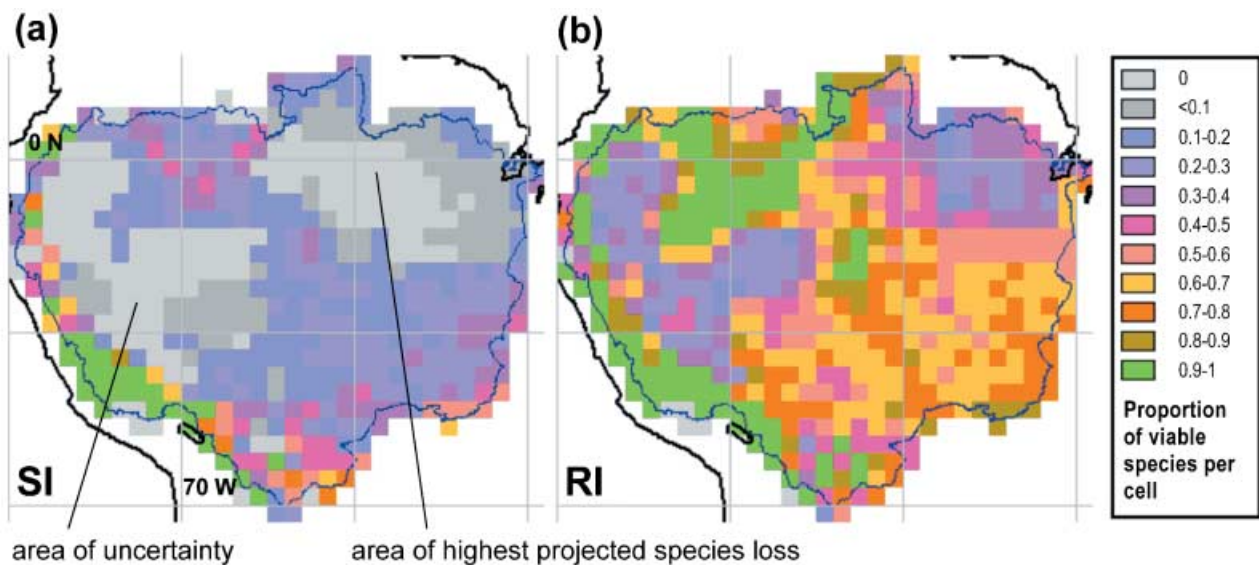


Figure 3 Proportion of species to retain viable populations at 2095 under (a) SI and (b) RI scenarios where 69 species have been modelled.

became nonviable. These were all tree species with small ranges.

Changes in the spatial distributions of seasonality and moisture deficit clearly affected species distributions. In both scenarios the most favourable habitats for moist forest species in 2095 were in the more aseasonal western Amazonia, and in high altitude areas, which are also concentrated in the west (Fig. 3). Accordingly, in the SI scenario, many species developed areas of new potential distribution along the western edge of their current simulated range. All three of the species currently restricted to western Amazonia, namely *Hirtella mutisii* (E.P. Killip and J. Cuatrecasas), *Chamaedorea fragrans* ((Ruiz & Pav.) Mart.) and *Nectandra reflexa* (Rohwer), retained at least one viable population in the SI scenario and gained new areas of potential distribution in the far west, though for *H. mutisii* the only new cell was disjunct from its existing populations. Of those species whose Amazonian distributions are currently restricted to central southern parts, *Tecoma tenuiflora*, *Tabebuia nodosa* and *Inga cardozana* (Sagot ex Benth.), only *T. nodosa* retained any viable cells in the SI scenario in 2095, although all three had limited new areas of potential distribution. The recorded range of *T. nodosa* extended into Paraguay's dry forests, whilst the southern distribution of *I. cardozana* clung more to the humid base of the Andes.

North-east Amazonia underwent the most profound long-term change in species density and composition. All of the modelled populations lost viability in the SI scenario, and only a small proportion remained viable in the RI scenario (see Fig. 3). Only two of the 69 species, the palms *Astrocaryum sciophilum* ((Miq.) Pulle) and *Geonoma oldemanii* (Granv.), had Amazonian distributions that were originally confined to this area, and so these might have been under greatest threat from local climate change. Both had extensive potential distributions in 1990, but as they are also found outside Amazonia, and these parts of their distributions were not modelled, it was difficult to reach any firm conclusions about their future viability. Neither retained a viable *in situ*

population in the SI or RI scenarios, but both gained new areas of potential distribution in north central Amazonia in the RI scenario.

Species that were widely distributed in Amazonia showed the greatest resistance to change, while those with narrow ranges or poor tolerance of moisture deficits changed the most. Indeed, spatial distribution appeared to be the most decisive factor in explaining species response, and although there was no clear relationship, a species needed to occupy at least 88% of all cells in inclusive Amazonia in 1990 to retain a large proportion of viable cells by 2095 in the SI scenario. As distribution is partly a surrogate for environmental range, species with considerable tolerance of variation in each bioclimatic variable were also most resistant to change. About two-thirds of the 69 species were widespread in 1990 and restricted only from occupying the cooler southern and/or western edges of the region.

Moist forest species that in the SI scenario gained new potential distributions on the western edge of their ranges, but lost viability over much of their existing range, included *Astrocaryum murumuru* (Mart.), *Oenocarpus bataua* (Mart.), *Socratea exorrhiza* ((Mart.) H. Wendl.), *Callichlamys latifolia* ((Rich.) K. Schum.), *Hirtella triandra* (Sw.), *Licania heteromorpha* (G. Bentham), *Inga alba*, *I. cayennensis* (L. Cárdenas), *I. marginata* (Willd.) and *I. nobilis* (Willd.). *Iriartea deltoidea* (Ruiz & Pav.) has such a wide environmental tolerance that its 1990 potential distribution covered all but the southern and western edge of Amazonia. Its realized distribution was restricted by buffering to the west and central regions. In the SI scenario, by 2095 it retained viable populations only in north-west Amazonia and along the south-western edge, but in the RI scenario it remained viable over most of its range, although areas with only relictual populations did appear in the east.

In the SI scenario, of the five species traits used to define PFTs only height class significantly affected the mean change in density of a species (Fig. 4). This is a strong determinant of generation

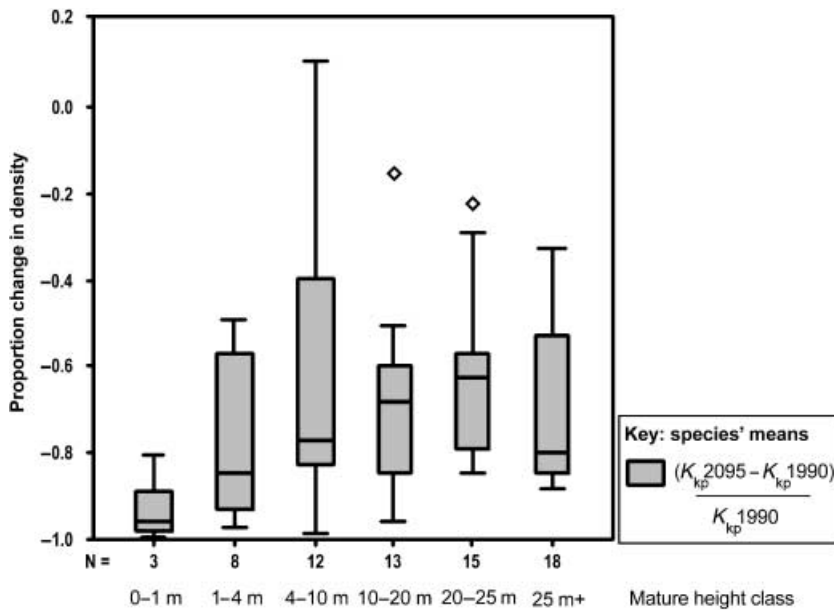


Figure 4 Species' mean change in density of mature individuals as a proportion of 1990 values (ΔK_{kp}), from 1990 to 2095, by height at maturity, in the SI scenario. SPSS box plot showing inter-quartile range (boxed), maximum and minimum non-outliers (whiskers) and outlier values (diamonds).

time, and therefore of the lag in population response to climate change. Species of small adult stature are under a more immediate threat than larger plants because they tend to have smaller ranges (Ruokolainen & Vormisto, 2000), attain adulthood more quickly and are dispersed over shorter distances.

CONCLUSIONS

We believe that this is the first systematic attempt to simulate the possible impacts of global climate change on the spatial distribution of species diversity in Amazonia. Ideally, the distributions of thousands of randomly selected species would have been simulated, but as this was not possible, for reasons of both logistics and lack of data, a stratified sample of species was chosen to be as representative as possible of functional and taxonomic biodiversity.

The results of the simulations were quite striking. Although there was no major change in the realized distributions of most species by 2095, because of population response lags, 43% of species had become nonviable in the SI scenario by that time because their potential distributions had changed drastically. The greatest change was in the north-east Amazonia, which experienced the most severe shift in precipitation and seasonality. Species that are now widely distributed in Amazonia showed the greatest resistance to change, while those with narrow ranges were the most vulnerable. Species in the smallest adult height classes were more vulnerable than larger trees, because their shorter generation time reduced the lag between when their population became nonviable in an area and when it actually disappeared. These simulations of future trends are the best that can be produced at the moment, given the widespread lack of data on species distributions in tropical moist forests. More robust findings must await the provision of better quality data.

There is a zone of projected increased AET in the west, which increases uncertainty in the model outputs (see Fig. 3). The stringent assumption was applied that a species cannot survive in the long term when climate values fall outside its recorded range. This

model indicates that no species can survive where AET increases to levels outside the recorded Neotropical range, as is seen in some cells under the SI scenario. In reality, high AET conditions are potentially highly productive, so we would expect the decrease in the proportion of viable populations to be less severe than that of the surrounding forest.

It is likely that many aseasonal moist forest species would find climate change refugia in this western zone. This region and the regions of increased MD in the north-east should therefore be key targets for monitoring the incidence and impact of climate change. They are modelled as undergoing the most extreme increases in AET and MD, respectively. Competitive displacements would be expected in the western zone, and decline of forest species in the north-eastern zone.

The model did not incorporate the direct effects of warming and/or carbon dioxide fertilization on plant physiology. There is empirical evidence that turnover (mortality and recruitment) of trees in Amazonian forests has accelerated in the last two decades (Phillips & Gentry, 1994; Phillips *et al.*, 2004), possibly in response to a global atmospheric or climatic driver (Lewis *et al.*, 2004). If these population processes continue to accelerate, the model results are likely to be over-optimistic about the ability of species to persist *in situ* once $S_p < S_{min}$.

These results have various implications for practical strategies to ameliorate the worst impacts of climate change on biodiversity. Area selection protocols for prioritizing forest conservation have become increasingly sophisticated (e.g. Myers *et al.*, 2000), but are still based essentially on combined assessments of current patterns of endemism and species richness, or present distributions of endangered ecosystem types. Our analysis provides some clues as to where effort should be focused in the Neotropics to retain those parts of species' ranges that would still be suitable under the projected changed conditions. The best remaining refugia for lowland moist forest species would be on the western edge of Amazonia, adjacent to the Andean highlands, though migrating species could also displace the existing diverse montane

forest flora. The latter are likely to be driven up their local altitudinal and moisture gradients, with the possibility of multiple extinctions as they encounter land use and topographical barriers, or simply reach the summit (Pounds *et al.*, 1999; Bush, 2002). So while it is vital to strengthen and expand protected area networks in the western Amazon Andean foreland plains, these networks must encompass a wide altitudinal gradient. This does not imply that reserves outside these areas should be discarded. Indeed, given the high level of uncertainty attached to projections of future climate change, the small fraction of Amazonian species considered here, and the many ecosystem services provided by tropical forests, as much forest should be conserved in Amazonia as possible, preferably in reserves that include both lowland and montane forests.

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BIOSKETCHES

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