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RESEARCH PAPER

Biodiversity loss under existing land use and climate change: an illustration using northern South America

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ABSTRACT

Aim Species richness depends on climate and land use. Maintaining locations with favourable climate and land-use patterns is critical for protecting biodiversity because the loss of either can reduce the species richness that an area supports. Currently, the Guiana Shield (GS) receives abundant precipitation and has relatively light land use. For species richness this constitutes a good–good combination of climate and land use, respectively. In contrast, much of eastern Brazil receives low levels of precipitation and has heavy land use, which is a bad–bad combination for species richness. Thus, the current distribution of precipitation and land use in northern South America is relatively favourable for biodiversity. Palaeoclimate and model studies suggest, however, that the precipitation patterns for the two regions have switched before and could switch in response to greenhouse gas emissions. This paper examines the potential consequences of reconfiguring climate with respect to existing land-use patterns using South America as an example.

Location South America north of 20° S and east of the Andes.

Methods Ecosystem structure and function are modelled under (1) historical climate and (2) altered precipitation following a shift in the location of the Inter-Tropical Convergence Zone (ITCZ). The distribution of precipitation, biomes, net primary productivity (NPP) and land use are then used to predict levels of species richness under the two climate scenarios.

Results Climate changes could shift the distribution of vegetation and NPP such that conditions favourable for species richness in the GS region disappear. If land-use patterns were not prohibitive in eastern Brazil, the improved climate conditions there could compensate for the GS loss (assuming migratory barriers are overcome). Instead, existing land-use patterns cause the combined species richness projected for the two regions to plummet.

Main conclusions Human activities will alter current configurations of land use and climate throughout the world. For species richness, new configurations are likely to include both positive and negative combinations of climate and land use. However, the irreversibility of past extinctions due to land-use patterns loads the dice against species richness.

Keywords

Biodiversity, biological impact, climate change, Inter-Tropical Convergence Zone, land use, net primary productivity, nonlinear climate response, South America, species richness.

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INTRODUCTION

Land-use disturbance and climate change constitute two separate threats to biodiversity (Sala *et al*., 2000; McLaughlin *et al*., 2002). In addition, land-use disturbance and climate change can directly interact to compound threats to biological systems. For example, development in urban, suburban, rural and agricultural areas imposes migratory barriers on species that will need to move to react to climate change.

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The need for species ranges to shift in response to climate change also raises the potential for a redistribution of biological systems with respect to land-use patterns. Those species that do overcome the migratory barriers may end up with new ranges that are either more or less heavily influenced by land-use patterns, relative to their current ranges. Understanding the implications of this redistribution of climate and land-use patterns will be critical for determining how biological diversity responds to future changes, particularly in the tropics where maximum levels of biodiversity occur.

The influence of climate in northern South America

Under current conditions (averaged between 1961 and 1990), precipitation north of 20° S and east of the Andes ranges from a low in eastern Brazil of roughly 500 mm year^{-1} to highs of roughly 3500 mm year^{-1} in central Amazonia (Fig. 1a, adapted from New *et al*., 1999). The distribution of vegetation tracks annual and seasonal precipitation patterns closely as evergreen forest occurs where precipitation is abundant, but drought deciduous forest, savannah, grassland and shrubland become increasingly common as precipitation decreases in eastern Brazil (Ramankutty & Foley, 1999). Field surveys also demonstrate that plant species richness tends to increase within this precipitation range (Gentry, 1988; Clinebell *et al*., 1995; De Oliveira & Daly, 1999; Pitman *et al*., 2002b) as does species richness among higher taxa (Voss & Emmons, 1996).

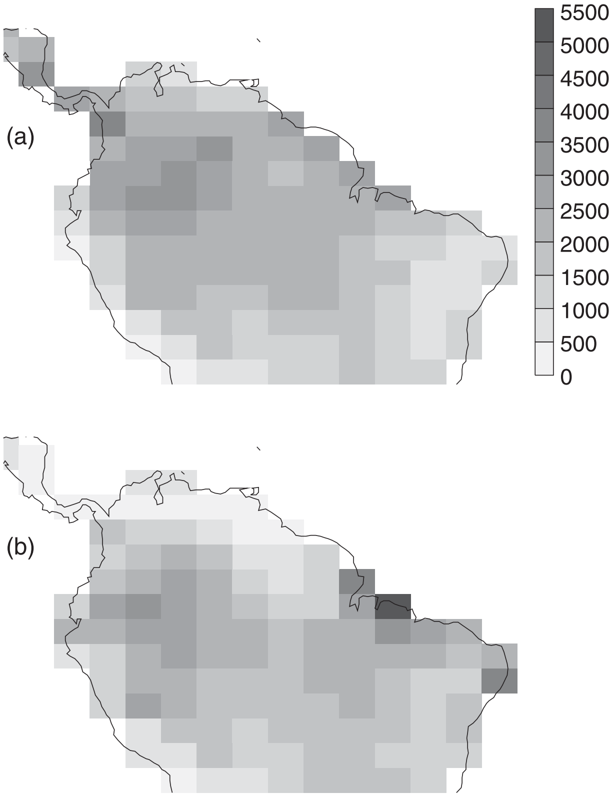

Figure 1 Mean annual precipitation for South America north of 20° S (mm year^{-1}) (a) historically averaged over the last few decades (adapted from New *et al*., 1999) and (b) as a consequence of a southward shift in the ITCZ (adapted from Vellinga & Wood, 2002).

The Guiana Shield (an area that includes all of Guyana, Suriname and French Guiana, and that extends from Colombia and Venezuela in the west to include portions of Brazil in the east), in particular, is hugely diverse biologically. The region contains roughly 25% of the world's remaining tropical evergreen forest and has roughly 20,000 vascular plant species (7000 endemics), 2200 fish species (700 endemics) and 1000 bird species (150 endemics) (Guayana Shield Conservation Priority Setting Workshop, 2002). As a result, the Guiana Shield (GS) is one of the most important centres of species richness on the planet.

Palaeoclimate records demonstrate, however, that precipitation patterns and species distributions in northern South America have changed throughout the past (Mayle *et al*., 2000; Ledru *et al*., 2002; Marchant *et al*., 2002), particularly in response to shifts in the location of the Inter-Tropical Convergence Zone (ITCZ) that may have resulted from changes in the ocean's thermohaline circulation (THC). Furthermore, some climate models suggest that changes in precipitation patterns and vegetation in northern South America (Betts *et al*., 1997; Johns *et al*., 2003) or the strength of THC in the North Atlantic (IPCC, 2001) may accompany changing greenhouse gas concentrations, although this is currently considered a low-probability event. In the climate model HadCM3, the GS becomes drier and eastern Brazil becomes wetter under weak THC (Fig. 1b, adapted from Vellinga & Wood, 2002). Changes such as these would alter net primary productivity (NPP) and the distribution of vegetation in the region and could therefore affect the distribution of species richness.

Current land-use patterns

Human population density is high in eastern Brazil and relatively low throughout much of the GS (CIESIN *et al*., 2000). Not surprisingly, land use and population density are linked, such that habitat is relatively less disturbed in much of the GS and heavily disturbed throughout eastern Brazil (UNEP and WCMC 2002) — here disturbance is defined as a measure of remoteness from human activity assessed on the basis of distance from settlements, access routes and permanent human structures (UNEP and WCMC, 2002). This is most clearly evident for croplands and pasture (Fig. 2, adapted from Ramankutty & Foley, 1998; Foley *et al*., 2005). Thus, the GS, which has large contiguous areas with little human land use, is one of the largest expanses of undisturbed rainforest. Eastern Brazil, in contrast, is characterized by few remote areas.

Low to intermediate levels of disturbance can increase species richness by increasing habitat heterogeneity or decreasing competitive exclusion (Connell, 1978; Huston, 1979). However, at the large scales of disturbance that characterize human activities in urban environments, particularly eastern Brazil, species richness generally declines (Estrada *et al*., 1997; Sala *et al*., 2000; Daily *et al*., 2001; Pitman *et al*., 2002a). Similarly, we can expect the responsiveness of species richness to the amount of precipitation an area receives to decrease under heavy levels of land use since species capable of existing under particular climate conditions

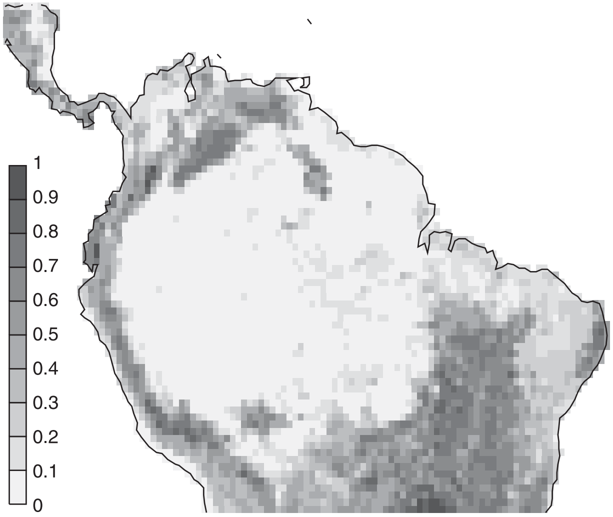

Figure 2 Fraction of land within each grid cell used for cropland or pasture (adapted from Ramankutty & Foley, 1998; Foley *et al.*, 2005). This does not include buildings, urban areas or other sources of human land-use disturbance.

become increasingly constrained by degraded or insufficient habitat.

A relationship between productivity and species richness is also widely reported throughout much of the world, with the highest levels of species richness tending to occur at intermediate levels of productivity (Rosenzweig, 1995). In sub-Saharan Africa, for example, a peak in species richness occurs at NPP values of roughly 0.8–1.1 kg C m^{-2} $year^{-1}$, with lower and higher NPP values leading to lower levels of species richness (Balmford *et al.*, 2001). Nevertheless, the ubiquity of this relationship remains controversial, with hump-shaped and positive relationships between productivity and species richness both commonly occurring (Mittelbach *et al.*, 2001).

Here I examine the implications for species richness of climate change within the context of pre-existing land-use patterns. I use a plausible shift in the location of the ITCZ for the region of South America north of 20° S and east of the Andes that suggests that simply shifting climate characteristics against existing land-use patterns may result in large losses of species richness.

METHODS

I develop two precipitation scenarios for northern South America to test structural and functional ecosystem responses to plausible climate changes at a broad spatial resolution (2.5° latitude by 3.75° longitude). The two climate scenarios are (1) a control (Fig. 1a), in which precipitation remains at historical monthly mean values from 1961 to 1990 (New *et al.*, 1999) and (2) a shift scenario (Fig. 1b), in which the maximum proportional changes in monthly mean precipitation modelled by HadCM3 (Vellinga & Wood, 2002) in response to a THC-induced southward shift in the ITCZ, described above, are added to the control precipitation values.

To examine potential NPP and vegetation distribution under each precipitation scenario I use the Integrated Biosphere Simulator (IBIS 2.6), a process-based dynamic global ecosystem model that has been extensively validated for its projections of ecosystem structure and function such as current distribution of vegetation, NPP, biomass, below-ground carbon cycling, evapotranspiration, runoff and leaf area (Foley *et al.*, 1996; Delire & Foley, 1999; Kucharik *et al.*, 2000). As previously described (Higgins & Schneider, 2005), IBIS represents vegetation in broad categories or plant functional types (PFTs) that differ in basic form (trees, shrubs or grasses), leaf type (broadleaf or needleleaf), patterns of leaf display (evergreen or deciduous) and photosynthetic pathway (C_3 or C_4). The relative success of different PFTs is determined by annual carbon balance. Trees, shrubs and grasses compete for light and water, with trees able to capture light first and shrubs and grasses better able to access water in the upper soil layers. PFTs with the same basic form differ in their ability to take up and respire carbon as a function of leaf form, seasonal patterns of leaf display and photosynthetic pathway.

IBIS requires input data for soil texture (Global Soil Data Task Group, 2000) and monthly climate characteristics, including average temperature, precipitation, relative humidity, cloudiness, temperature range, wind speed and number of rainy days. IBIS then uses a weather generator to produce daily variability from the monthly climate input. In these simulations, monthly average precipitation is developed as described above. All other climate data come from historical climatology from 1961 to 1990 (New *et al.*, 1999) averaged for the 2.5° latitude by 3.75° longitude cells corresponding to the spatial resolution of HadCM3. The climate changes represented by the precipitation shift scenario would also alter climate variability. As a result, this approach, which changes only monthly mean precipitation, does not allow feedback on other parameters of the weather generator.

The changes in sea surface temperature that cause this ITCZ shift would also be likely to influence temperature patterns throughout the region. Furthermore, precipitation and temperature influence one another by altering atmospheric circulation, relative humidity and evapotranspiration. Therefore, the precipitation change scenario is not entirely physically consistent. Past research demonstrates, however, that the small changes in temperature associated with this climate change scenario do not alter the response of vegetation in this region and that precipitation changes alone are sufficient for accurately characterizing the response of the vegetation (Higgins & Vellinga, 2004).

In these simulations, carbon dioxide concentration remains constant (350 p.p.m.). Physiological responses to elevated CO_2 concentrations would be likely to affect ecosystem structure and function by altering rates of photosynthesis, respiration and water use efficiency (Mooney *et al.*, 1999; Korner, 2000). Incorporating the most widely demonstrated plot-level responses to CO_2 enrichment (Nowak *et al.*, 2004; Norby *et al.*, 2005) into model simulations would be likely to lead to decreased plant water stress and increased NPP and carbon storage, as previously discussed (Higgins & Harte, 2006). However, recent experiments suggest that the effects of CO_2 enrichment on ecosystems will

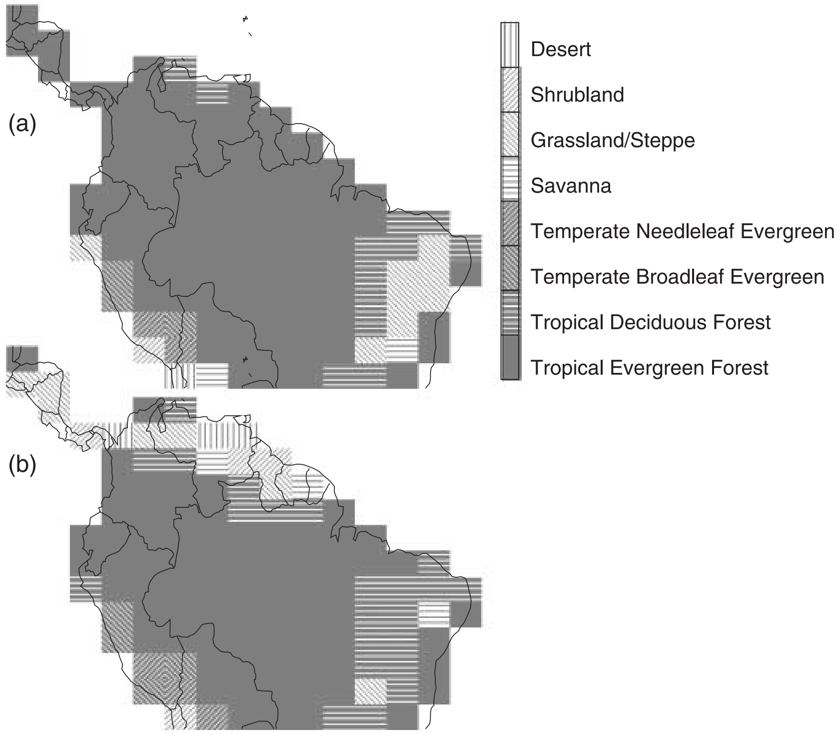

Figure 3 Modelled biome distribution for South America north of 20° S. (a) Under current climate conditions rainforest occurs throughout much of the Guiana Shield while drier biomes dominate in eastern Brazil. (b) The southward shift in precipitation causes forest loss and a transition to drought deciduous forest throughout much of the Guiana Shield, while forest expansion occurs throughout much of eastern Brazil.

be far more complex than conventional single-factor CO$_2$ manipulation experiments have demonstrated, because additional factors (e.g. changes in temperature, precipitation, and nitrogen availability) interact to alter responses to CO$_2$ (Shaw *et al.*, 2002; Dukes *et al.*, 2005). IBIS does not yet incorporate multifactor effects, though this may change as the scientific community adopts alternative CO$_2$ enhancement functions as additional multifactorial experiments for a variety of ecosystem types become more widely available. Furthermore, scaling from the leaf and plot level responses that manipulative experiments reveal to the ecosystem scales that are most relevant to the climate system is extremely challenging. Until substantial improvements in our understanding occur, it makes sense to keep CO$_2$ constant at a value for which IBIS has been extensively validated (Delire & Foley, 1999; Kucharik *et al.*, 2000) and at which relationships between productivity and species richness have been examined.

Each IBIS simulation begins from a cold-start (i.e. without pre-existing vegetation) and with a 100-year spin-up under historical climatology. At the end of the 100-year spin-up, precipitation either experiences a step change or remains constant. IBIS then runs for an additional 100 years under each scenario to estimate longer-term ecosystem changes. This reveals near-equilibrium vegetation distribution and NPP for each scenario.

I compare annual NPP between the scenarios by averaging over the final decade of the experiment for each grid cell. The biome type for each scenario is determined using average leaf area index (LAI) for each PFT over the final decade and IBIS's annual biome classification scheme. The classification scheme distinguishes among biomes based on a grid cell's total LAI, dominant PFT (i.e. the one with the largest contribution to LAI) and the combination of other PFTs that occur in the grid cell (Foley *et al.*, 1996; Kucharik *et al.*, 2000). Averaging over the last decade reduces the potential for anomalies due to interannual variability generated by the weather generator. I then use the combination of precipitation, NPP and potential biome distributions to generate a simplified conceptual diagram that relates species richness, precipitation and disturbance in the region.

RESULTS

Under historical precipitation patterns, IBIS projects rainforest throughout much of the GS and a transition to drought deciduous forest, grassland and savannah in eastern Brazil (Fig. 3a). This agrees well with actual potential vegetation (Ramankutty & Foley, 1999), particularly at the coarse spatial resolution of the climate and topographical data used in these simulations. Under the climate change scenario, IBIS simulates forest loss and a transition to drought deciduous forest throughout much of the GS, while forest expansion occurs throughout much of eastern Brazil (Fig. 3b).

Under historical precipitation patterns, modelled NPP in much of eastern Brazil (Fig. 4a) ranges from 0.2 to 0.6 kg C m^{-2} year^{-1} while the abundant rainfall in the GS leads to NPP values typically ranging from 0.6 to 1.4 kg C m^{-2} year^{-1} with much of the region residing between 0.8 and 1.2 kg C m^{-2} year^{-1}. The southward shift in precipitation causes this NPP pattern to reverse such that much of the GS has NPP values under 0.6 kg C m^{-2} year^{-1}, while eastern Brazil has increasing NPP values that range from 0.6 to 1.2 kg C m^{-2} year^{-1} (Fig. 4b).

Figure 5 presents a simplified conceptual diagram of the relationship between species richness and precipitation under

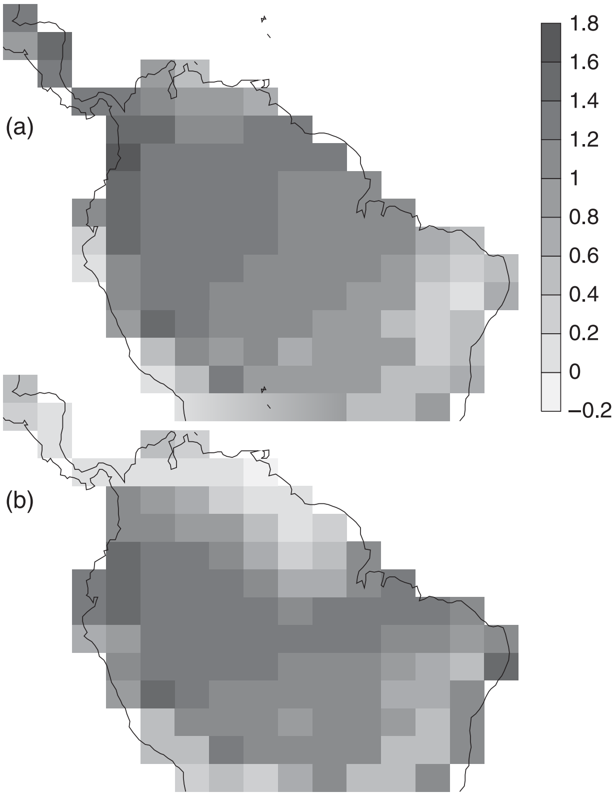

Figure 4 Modelled net primary productivity (kg C m^{-2} $year^{-1}$) generated (a) under historical climatology and (b) in response to a southward shift in precipitation. Currently NPP is high in the Guiana Shield and low in eastern Brazil, but this pattern reverses with a southward shift in precipitation.

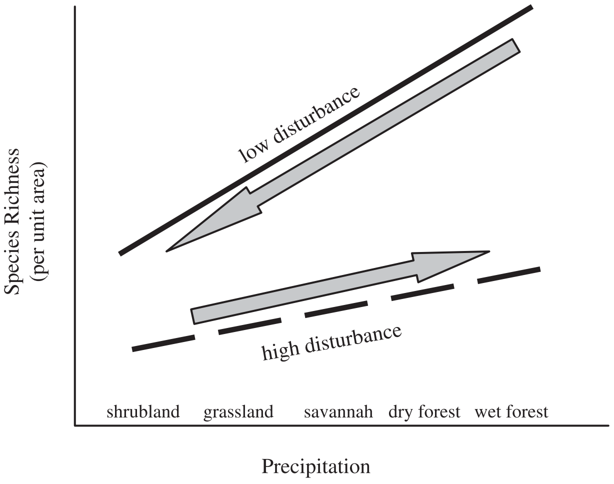

Figure 5 Highly simplified conceptual relationship between species richness and precipitation under variable human land use for South America north of 20° S and east of the Andes. Species richness tends to increase with precipitation, but heavy disturbance reduces species richness and the responsiveness of species richness to precipitation changes. The grey arrows indicate changes that occur due to the southward shift in precipitation. Under current conditions favourable climate and land-use patterns co-occur in the Guiana Shield (GS) while unfavourable conditions co-occur in eastern Brazil. Due to pre-existing land-use patterns, the loss in species richness in the GS region is greater than the potential gain in species richness in eastern Brazil.

heavy and light land use for the region. The diagram captures three critical features: (1) species richness tends to increase with precipitation; (2) heavy land use reduces species richness relative to light land use at any level of precipitation; and (3) the responsiveness of species richness to precipitation decreases with the degradation, destruction and fragmentation of habitat under heavy land use.

Currently, the GS receives high levels of precipitation, has intermediate to high NPP and has relatively light land use. For species richness, this constitutes a good–good combination of climate and land use, respectively, and fosters high levels of species richness (Fig. 5). In contrast, eastern Brazil receives sparse precipitation, has low NPP, and has high levels of land-use disturbance. This constitutes a bad–bad combination of climate and land use, respectively, and fosters lower levels of species richness. The arrows in Fig. 5 indicate the direction of changes that result from the southward shift in precipitation. The new configuration is characterized by climate conditions favourable for species richness occurring where land-use patterns are prohibitive (and vice versa). As a result, the losses in species richness in the GS are considerably larger than the gains in eastern Brazil.

DISCUSSION

Species ranges have already begun to move in response to the relatively modest climate changes of the past century (Parmesan & Yohe, 2003; Root *et al.*, 2003). As greenhouse gas emissions continue over the next century, biological systems will increasingly need to move in order to adapt to the ensuing changes in climate. As a result, the distribution of biological systems will shift relative to past land-use patterns.

The single climate change scenario examined here illustrates the potential for unfavourable reconfigurations of species ranges with respect to land-use patterns. In the GS region, precipitation and biome patterns favourable for species richness currently co-occur with relatively low levels of land use. Under the precipitation shift scenario, however, biome and precipitation patterns favourable for species richness in the GS region disappear. If land-use patterns were not prohibitive in eastern Brazil, species richness gains there could compensate for this loss (assuming migratory barriers are overcome). But existing land-use patterns prevent this potential gain even if species are able to overcome the barriers to migration they face. As a result, the species richness for the area as a whole would plummet under this scenario.

Modelled NPP values provide further confirmation of this conclusion. Under current conditions, NPP values are intermediate to high in the GS and considerably lower in eastern Brazil. Again, this is consistent with favourable climate patterns for species richness co-occurring with favourable land-use patterns in the GS and unfavourable conditions co-occurring in eastern Brazil. The precipitation shift leads to a reconfiguration of NPP with respect to land use, however, in which lower levels of species richness become favoured in the less disturbed GS region and higher levels of species richness become more suited to the heavily disturbed eastern Brazil. As a result of pre-existing land use, the loss of species richness in GS far outweighs the potential gain in eastern Brazil. This conclusion holds regardless of whether one assumes a positive relationship between NPP and species richness or a unimodal relationship. Thus, this is a robust conclusion.

The results from any single climate change scenario must be interpreted with caution, however, especially for changes in the hydrological cycle (IPCC, 2001). Weakening of the thermohaline circulation, in particular, is viewed as likely to be be a low-probability event. Nevertheless, many climate models do suggest that changes in ocean circulation may accompany increasing concentrations of greenhouse gases (IPCC, 2001) and similar precipitation changes occur in some of the simulations that use the IS92a and A2 future climate scenarios (IPCC, 2001; Johns *et al*., 2003). Furthermore, changes in precipitation and biome such as these appear throughout the palaeoclimate (Ledru *et al*., 2002) and pollen (Mayle *et al*., 2000; Marchant *et al*., 2002) records and recent evidence suggests that weakening of the THC may be under way (Bryden *et al*., 2005). Thus, the precipitation shift examined here appears consistent with a range of potential past and future climate change scenarios.

More importantly, the paper's broader conclusions do not depend on this single climate scenario because changes in climate will be likely to involve precipitation shifts in at least some locations, albeit in patterns that remain hard to predict. In some cases those shifts will involve reconfigurations of climate conditions with respect to land-use patterns. Thus, this single scenario is illustrative of the types of shifts that will occur under any climate change scenario in at least some locations.

Favourable recombinations of climate and land-use patterns may also occur in different regions or under other plausible climate change scenarios. For example, climate shifts could ease the conflict between biodiversity and human development by separating favourable climate conditions from unfavourable land-use patterns. As a result, species for which extinction is currently entrained due to land use may find the habitat they require for long-term recovery.

Past extinctions are irreversible, however, at least on time-scales relevant to human activities. As a result, historical land-use patterns act as a sieve for species richness: once gone a species (or population or individual) cannot return. This reduces the potential gains from favourable recombinations in climate and land-use patterns relative to the unmitigated losses that can occur from damaging recombinations like that shown here for northern South America. Furthermore, transient climate changes amplify the potential danger of reconfiguring climate and land-use patterns as even a temporary restriction of favourable climate to areas heavily disturbed by land use would act as a bottle neck for the long-term survival of some species. As a result, the irreversibility of extinctions due to land-use patterns loads the dice against biodiversity when climate changes.

Land-use patterns are also likely to change through time and perhaps even in response to changes in climate. Therefore, the assumption that land-use patterns would remain constant oversimplifies how human activities will be likely to respond to this, or any, climate change scenario. Agricultural abandonment may improve habitat quality in eastern Brazil, while land conversion will be likely to reduce habitat quality in the GS. Thus, including land-use change will be necessary to understand fully how biodiversity will respond to future change. However, the heavy land-use patterns that characterize eastern Brazil are unlikely to approach the low levels of disturbance that currently characterize the GS as roads, buildings and urban areas constitute long-term sources of disturbance.

These experiments examine near-equilibrium responses for biome distribution and NPP and therefore do not consider transient changes in climate or the dynamics of ecosystem responses, each of which could substantially influence species richness. This is a conservative approach, however, as barriers to migration (human caused or natural) in combination with rapid rates of environmental change can strongly influence ecosystem responses (Higgins & Harte, 2006) and are likely to further threaten species richness.

Similarly, other global changes (e.g. the direct effects of elevated CO_2, nitrogen deposition, invasions of exotic species, land-use change, etc.) will interact with climate change to amplify and dampen ecosystem responses in complex ways. Physiological responses to elevated CO_2 concentrations, in particular, may alter rates of photosynthesis, respiration and water use efficiency (Mooney *et al*., 1999; Korner, 2000) and thereby affect species distributions and richness. The most widely demonstrated plot-level responses to CO_2 enrichment (Nowak *et al*., 2004; Norby *et al*., 2005) imply that plant water stress would decrease and NPP would increase relative to the simulations presented here, as previously discussed (Higgins & Harte, 2006). Recent multifactorial studies suggest, however, that single factor manipulation experiments overestimate CO_2 responses, because interactions among the other factors (e.g. changes in temperature, precipitation and nitrogen availability) alter and dampen responses to CO_2 (Shaw *et al*., 2002; Dukes *et al*., 2005). Scaling from the leaf and plot level responses found in manipulative CO_2 experiments to the ecosystem scales examined here is also extremely challenging. Therefore, these experiments examine static ecosystem responses to changes in climate alone, for which our understanding of species-richness relationships are also more firmly established.

Issues related to spatial scale are also hugely important in determining species extinction, as species loss will depend on the spatial distribution of species within the GS, the presence or absence of habitat refugia following climate shifts and the spatial scale of interest. Indeed, evidence suggests that many tree species in Amazonia are widespread (Pitman *et al*., 1999). Thus, the local loss of species implied here does not necessarily translate to species extinction across broader spatial scales.

Nevertheless, this analysis demonstrates that losses of species richness would occur locally in northern South America in response to the combination of existing human land-use patterns and the ITCZ shift climate scenario studied here. Extrapolation from these results to a global scale implies that greenhouse gas emissions will be likely to cause the rearrangement of climate patterns with respect to land-use patterns with both positive and negative reconfiguration occurring in specific locations. The inherent irreversibility of extinction reduces the potential benefit of favourable recombinations, however. Therefore, climate change and land-use patterns will be likely to interact to reduce species richness even without overall changes in potential biome area or if species are able to overcome the migratory barriers they face from development in urban, suburban, rural and agricultural areas. As a result, biodiversity losses that would not have occurred in response to similar climate changes had they occurred in the past will occur over the next century.

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