



LETTER

Global congruence of carbon storage and biodiversity in terrestrial ecosystems

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Abstract

Deforestation is a main driver of climate change and biodiversity loss. An incentive mechanism to reduce emissions from deforestation and forest degradation (REDD) is being negotiated under the United Nations Framework Convention on Climate Change. Here we use the best available global data sets on terrestrial biodiversity and carbon storage to map and investigate potential synergies between carbon and biodiversity-oriented conservation. A strong association ($r_S = 0.82$) between carbon stocks and species richness suggests that such synergies would be high, but unevenly distributed. Many areas of high value for biodiversity could be protected by carbon-based conservation, while others could benefit from complementary funding arising from their carbon content. Some high-biodiversity regions, however, would not benefit from carbon-focused conservation, and could become under increased pressure if REDD is implemented. Our results suggest that additional gains for biodiversity conservation are possible, without compromising the effectiveness for climate change mitigation, if REDD takes biodiversity distribution into account.

Introduction

Conversion of natural ecosystems is the second largest source of human-induced climate change, accounting for 17–20% of anthropogenic greenhouse gas emissions (Gullison *et al.* 2007; Metz *et al.* 2007), and is the single most important driver of species extinctions (Baillie *et al.* 2004). Yet, despite major global scientific (Baillie *et al.* 2004; MEA 2005; Gullison *et al.* 2007; Metz *et al.* 2007) and political (United Nations 1992, 1993) backing for the importance of forests and other ecosystems for global climate regulation and biodiversity conservation, deforestation rates remain unabated (FAO 2006).

Conversion is now concentrated in the most carbon-rich and biodiverse biome on Earth, the tropical forests (FAO 2006). Recent research suggests that the role these forests play in global climate regulation might be greater than previously thought (Stephens *et al.* 2007; Bonan 2008; Lewis *et al.* 2009) and that some of its richest biodiversity hotspots are still poorly explored (Carnaval *et al.* 2009).

New studies have also highlighted that climate change, deforestation, carbon storage in biomass and biodiversity are closely interlinked. For instance, in addition to contributing directly to global warming, deforestation also makes forests more susceptible to the effects of climate change (Malhi *et al.* 2009; Phillips *et al.* 2009). Climate

change will be a major driver of future species extinctions (Thomas *et al.* 2004) and one of its possible feedbacks is a further depletion of forest carbon stocks (Malhi *et al.* 2009). Biodiversity, on the other hand, might alleviate some of these effects by making ecosystems more resilient (Reusch *et al.* 2005; Tilman *et al.* 2006) and, possibly, more productive (Flombaum & Sala 2008).

A landmark global deal being discussed under the United Nations Framework Convention on Climate Change is likely to include an international mechanism of financial incentives to reduce emissions from deforestation and forest degradation (REDD) (Gullison *et al.* 2007; UNFCCC 2007; Strassburg *et al.* 2009). As the estimated magnitude of the financial incentives being discussed (Kindermann *et al.* 2008; Strassburg *et al.* 2009) dwarfs current conservation expenditures in developing countries (James *et al.* 1999), REDD could trigger the biggest paradigm shift in conservation history. While it is generally assumed that REDD would have positive impacts for biodiversity conservation, this assumption has not been rigorously tested. Attention to the design of such a mechanism could enable increased gains for biodiversity, while reducing the risks, e.g., for those ecosystems that fall outside the scope of REDD (Miles & Kapos 2008). Better understanding of the congruence between carbon storage and biodiversity conservation would help to maximize the gains and better address the risks. Here we use high-resolution data to analyze for the first time the global congruence between carbon storage in biomass and biodiversity in order to investigate the synergies between climate- and biodiversity-oriented conservation.

Methods and data

Our analysis is based on three global data sets of the distribution of mammal (Schipper *et al.* 2008), amphibian (Stuart *et al.* 2004), and bird (Orme *et al.* 2005) species, totaling 20,697 species, and on a new global carbon data set (Ruesch & Gibbs 2008). The carbon data set presents estimates of above- and below-ground (root) biomass, and is the first to apply consistently the IPCC Good Practice Guidance (Penman *et al.* 2003) to the whole terrestrial surface. We investigated the congruence between carbon and each of three biodiversity indices: richness (number of species per cell), threat (number of threatened species per cell), and range-size rarity (number of species per cell whose ranges are in the lowest quartile for their class—see Supporting Information for details).

All data (described and discussed in the Supporting Information) were analyzed on a geodesic discrete global grid system, defined on an icosahedron and projected to the sphere using the Inverse Snyder Equal Area (ISEA)

Projection (Sahr *et al.* 2003). This corresponds to a hexagonal grid composed of individual units (cells) that retain their shape and area ($\sim 12,500$ km², similar to a 1×1 degree rectangle at the equator) throughout the globe. These are more suitable for a range of ecological applications than the most commonly used rectangular grids (Birch *et al.* 2007). The analysis was conducted on a subset of this global grid: all 15,018 cells containing any land.

The range of each species was converted to the hexagonal grid for analysis; a species was assumed to be present in a given cell if any part of the cell overlapped the species' mapped range. For each cell: a Richness Index was calculated as the total number of species mapped in the cell (Figure S1A); a Threat Index was calculated as the number of threatened species per cell (Figure S1B); and a Restricted-Range Index was calculated as the number of restricted-range species (the 25% species in each taxon with the smallest range size) per cell (Figure S1C). Carbon data were also converted to the hexagonal grid, with the value in each cell corresponding to mean carbon density for the land area (Figure S2).

Congruence between carbon and biodiversity was investigated visually (through maps) and analytically (through correlations). Global maps of the relationship between carbon and each of the biodiversity indices (Figure 1) were produced by plotting each hexagon with a color defined on a two-dimensional scale (Williams & Gaston 1998), with intensity on the blue axis defined using the carbon density and intensity on the red axis defined from the biodiversity index. The color scales are based on statistical distribution of the data: a linear scale is used for values falling between minus three standard deviations and plus three standard deviations. Any cells with values outside this range are grouped into single color bands and the ends of the scale. Maps were plotted using GMT software (Wessel & Smith 1998). Spearman's rank (r_s) correlation coefficients were calculated for the relationship between carbon and each of the biodiversity indices (Table 1), and their tests accounted for possible spatial autocorrelation (see Supporting Information).

Results and discussion

Overall, our results support the expectation that mechanisms for conserving biomass carbon (such as REDD) would have substantial cobenefits for biodiversity, and vice versa. Indeed, we found high congruence between species richness and biomass carbon at the global level ($r_s = 0.82$, Table 1; Figure 2A). This result is not unexpected, given that on the one hand biodiversity-poor ecosystems such as most deserts and polar regions are

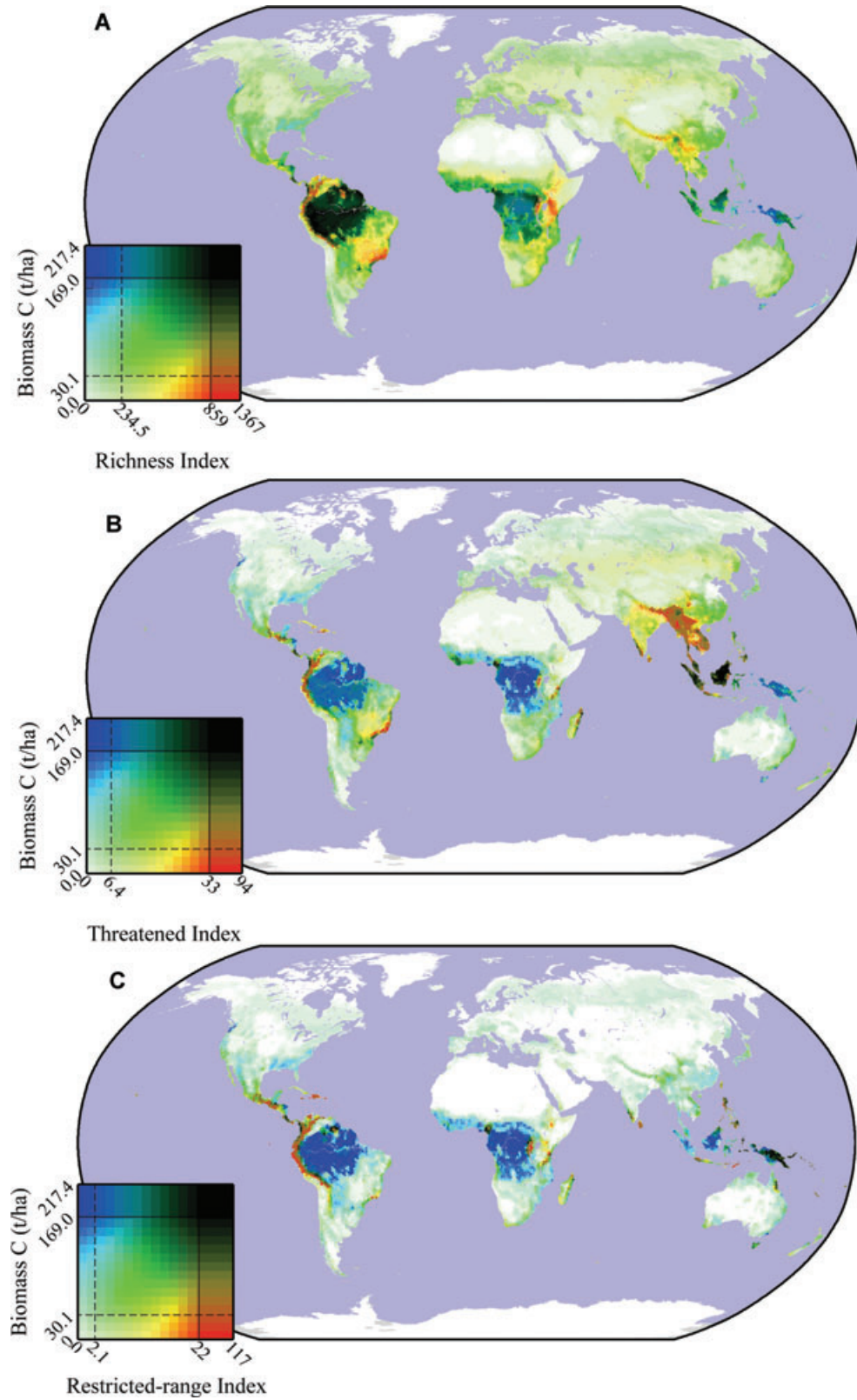


Figure 1 Global congruence between biomass carbon and overall species richness (A), threatened species richness (B), and restricted-range species richness (C). The two-dimensional color scale used displays both the concentration of biomass carbon and biodiversity and the congruence

Table 1 Correlations between carbon biomass and biodiversity for each of the biodiversity indices considered (Richness, Threat, and Restricted Range) and for either all species or for each of the taxa (amphibians, birds, or mammals) separately. r_s is Spearman rank correlation coefficients of all cells, EDF is Dutilleul-corrected degrees of freedom for the first r_s coefficients; P -values are the corresponding max P -values; r_s nonautocorr present the mean and the 95% confidence intervals of Spearman rank correlation coefficients for replicates of subsets of cells 1,400 km apart from each other for which spatial autocorrelation is negligible (see supporting information)

	Richness index				Threat index				Restricted range index			
	r_s	EDF	P -values	r_s non-autocorr	r_s	EDF	P -values	r_s non-autocorr	r_s	EDF	P -values	r_s non-autocorr
All species	0.82	53.8	<0.0001	0.73 (0.59–0.83)	0.55	68.4	<0.001	0.39 (0.21–0.54)	0.42	149.3	<0.001	0.36 (0.17–0.52)
Amphibians	0.84	51.0	<0.0001	0.77 (0.68–0.83)	0.37	250.6	<0.0001	0.35 (0.19–0.48)	0.24	357.5	<0.01	0.22 (0.06–0.35)
Birds	0.80	57.6	<0.0001	0.71 (0.58–0.81)	0.43	73.8	<0.01	0.28 (0.09–0.47)	0.38	149.5	<0.001	0.32 (0.10–0.51)
Mammals	0.79	54.3	<0.0001	0.69 (0.56–0.78)	0.52	64.7	<0.001	0.38 (0.22–0.49)	0.31	266.2	<0.001	0.29 (0.11–0.46)

also carbon-poor (shades of white and pale green in Figure 1A), and on the other hand tropical forests (particularly the Amazon) are rich in both carbon and species (dark tones in Figure 1A).

There are also synergies between conservation of threatened or restricted-range species and carbon-based conservation (Table 1), but these are less striking (at least at the global scale). Indeed, we found moderate congruence between biomass carbon and threatened ($r_s = 0.55$, Figure 2B) and restricted-range ($r_s = 0.42$, Figure 2C) species. This is probably at least partially explained by the fact that although the two largest expanses of tropical forest (the Amazon and the Congo Basin) have simultaneously high carbon densities and species richness (hence high congruence in Figure 1A), they have relatively few restricted-range or threatened species. The coarse scale of our analysis is also likely to reduce the congruence between carbon and rare and threatened species by masking finer scale relationships in some areas (see below). In addition, prioritizing regions under threat of conversion (as a carbon mechanism would likely do) would likely substantially increase the correlation with threatened species

The regional patterns identified in Figure 1 show a wide variation in synergies among carbon and biodiversity conservation, with correspondingly varied policy implications. Some areas would provide a high degree of cobenefits for the goals of conserving biomass carbon and biodiversity, including areas of high congruence between carbon and overall species (e.g., the Amazon; Figure 1A), threatened species (e.g., Indonesia; Figure 1B), and endemic species (e.g., New Guinea; Figure 1C). Some areas

that are of high priority for one of the conservation objectives but have moderate importance for the other could still benefit from complementary financing from this second one. For example, Mainland Southeast Asia, a priority for biodiversity conservation, could benefit from complementary funding from carbon conservation. Finally, regions that are of high priority for one of the goals but of low importance for the other deserve careful consideration to ensure that they are not neglected. In particular, if a large-scale carbon-focused REDD mechanism is implemented, biodiversity-rich and relatively carbon-poor regions could suffer from a double conservation jeopardy, with conservation investment diverted away from them, and human pressure redirected toward them, as carbon-rich areas become the focus of conservation efforts. Areas potentially at risk include some that are widely recognized as global biodiversity conservation priorities such as the Brazilian Cerrado, the Cape Floristic province, and the Succulent Karoo (Mittermeier *et al.* 2004).

In some regions, the lack of congruence between carbon stocks and biodiversity might be an artifact of the coarse scale of our spatial analysis (Figure 3). Extensive deforestation often leaves remaining natural habitats concentrated in sparse forest fragments. These regions have low carbon per 1° cell, but each remaining forest fragment can be carbon-rich on a per-forest area basis. Habitat loss means many of these forests' species will be threatened, particularly if their ranges are small. Hence these regions might emerge in our coarse-scale analysis as having low carbon per cell, yet high counts of threatened or range-restricted species. If mapped at a

between them. The intensity on the vertical blue axis represents biomass carbon density (tons of C per hectare) and the intensity on the horizontal red axis the richness of the respective biodiversity index (number of species per cell). Darker shadings correspond to higher concentrations. Colors along the 45° diagonal (white-to-green shading) indicate high congruence between biomass carbon and biodiversity. Areas with low congruence are represented by colors along the white-to-blue (higher carbon, lower biodiversity) or white-to-red (higher biodiversity, lower carbon) axes. The color scales are based on statistical distribution of the data: a linear scale is used for values falling between minus three standard deviations and plus three standard deviations. Any cells with values outside this range are grouped into single color bands at the ends of the scale.

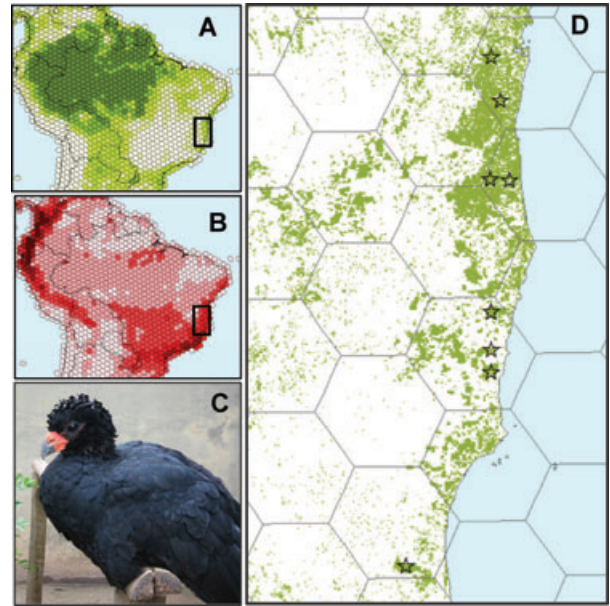
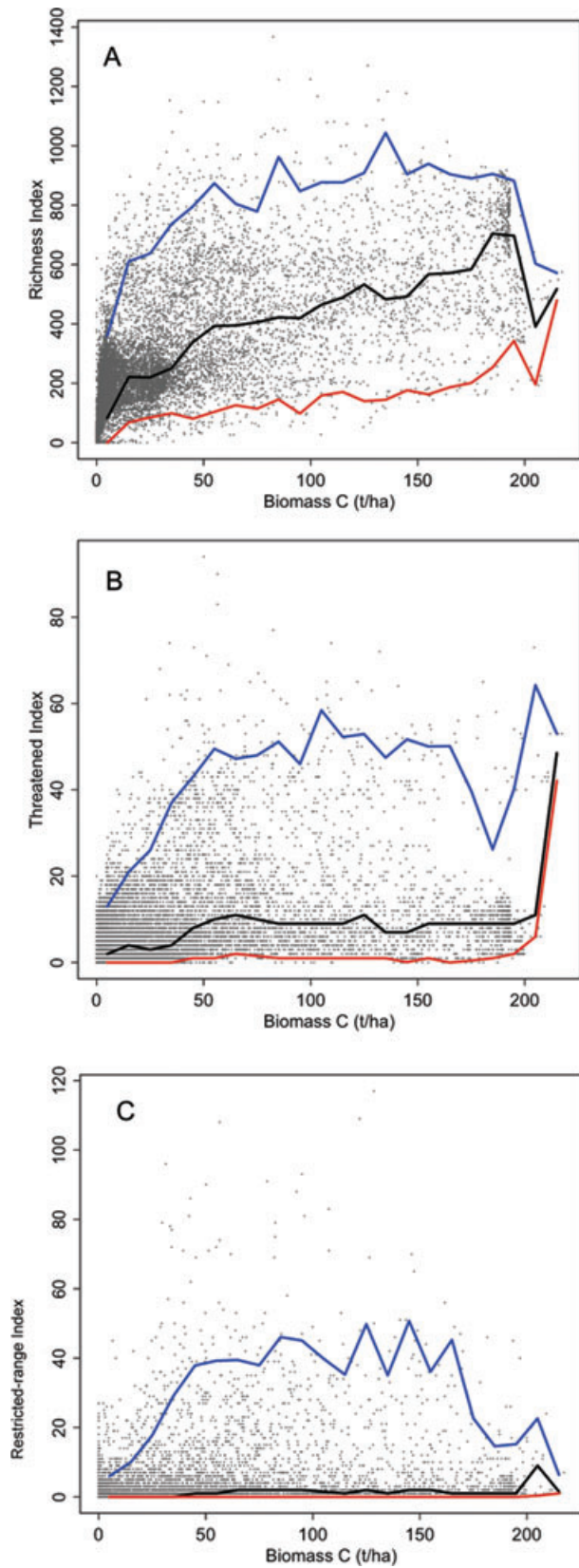


Figure 3 An illustration of the effect of scale on the congruence between carbon and biodiversity in fragmented areas. At the spatial resolution employed in our analyses (cells $\sim 12,500 \text{ km}^2$), the Atlantic Forest of South America (part of which is outlined by a box) emerges as an area of low congruence between carbon and biodiversity, appearing to contain relatively low carbon (A; shades of green correspond to carbon per cell) but high biodiversity value, for example, in terms of numbers of threatened species (B; shades of red correspond to number of threatened species per cell). At finer scales, though, the congruence is much higher, as most of the species that give this region its exceptional biodiversity value are restricted to the remaining fragments, corresponding to 7% of the original forest cover (Carnaval *et al.* 2009), which are carbon-rich. The endemic and Endangered Red-billed Curassow (*Crax blumenbachii*), for example, (C; photo by Alberto Teleuko, Wikimedia Commons), is only known from a few forest patches (D, inset; stars—species' records; green—forest fragments) (Bird Life International 2008). We believe that these fragmented areas provide some of the most valuable opportunities for “win-win” carbon and biodiversity conservation.

finer scale, they might instead be identified as small fragments of high value for both carbon and biodiversity, surrounded by a matrix of low carbon and low biodiversity. This is almost certainly the case of parts of the Atlantic Forest of South America, the Tropical Andes, and Southeast Asia (Figure 1B). Often, those remaining

Figure 2 Global scale relationship between biomass carbon and overall species richness (A), threatened species richness (B), and restricted-range species richness (C). In addition to all 15,018 individual data points, each panel presents an envelope containing 95% of the cells. To construct the envelope, cells were grouped based on their carbon content (each group being 10 tons of carbon wide). For each group the extremes were then excluded, with the cells with the highest or lowest 2.5% number of species falling outside the upper (blue line) or lower (red line) bounds, respectively. The black line represents the mean number of species of each group.

fragments are also highly threatened from future deforestation, and so their conservation would provide high benefits in terms of both avoided emissions and avoided extinctions. Future analyses at finer scale would be able to better capture these relationships. This refinement would be especially important to investigate the synergies between carbon-oriented conservation and threatened and rare species, and in particular for species that are both rare and threatened, maybe the most valuable group for biodiversity conservation (Ricketts *et al.* 2005).

We have also calculated correlation coefficients between carbon and biodiversity indices (richness, threat, and restricted range) separately for each of the taxonomic groups (amphibians, birds, mammals) (Table 1). We found that the results are consistent with those found for the overall biodiversity indices, demonstrating that they are not driven by any particular taxon among those analyzed, and suggesting that they are robust to the choice of taxa as surrogates of biodiversity. However, some areas have very high value for biodiversity conservation despite having lower vertebrate diversity (see Supporting Information).

We investigated the effect that spatial autocorrelation has on our results through three different approaches (Tables S1–S3 and Supporting Information). Although most correlation coefficients go down when redoing the analyses for sets of non-autocorrelated samples (Table 1 and Table S2), the decreases are relatively small (e.g., for Species Richness, nonautocorrelated r_S is 0.73, down from 0.82 for total cells). Most importantly, all coefficients have P -values < 0.01 even when controlling for spatial autocorrelation and none of the conclusions or relative comparisons discussed is affected.

Our analysis was focused on carbon stored in above- and below-ground biomass only. The soil carbon pool is 4.5 times the biotic carbon pool (Lal 2004). But unlike biomass carbon, there is no agreement on the magnitude or even the sign of the change in this pool following land-use change (Guo & Gifford 2002), which varies greatly depending on several factors (e.g., replacement land cover). Therefore it is not possible to assess the importance of soil carbon stocks for climate change mitigation without taking into consideration a dynamic land-use context. For these reasons, we opted to focus our analysis on biomass carbon, the primary carbon pool affected by land cover change. Nonetheless, a sensitivity analysis whereby total carbon is measured by adding biomass carbon and 25% of the soil carbon stock (Figure S3 and Supporting Information) showed only a relatively small decrease in correlation between vulnerable carbon and species richness ($r_S = 0.73$, down from $r_S = 0.82$).

Our analysis is about carbon stock (that can be lost due to land conversion) and it fails to include the value

of different ecosystems for carbon sequestration. There is now clear evidence that mature forests, both tropical (Phillips *et al.* 2008; Lewis *et al.* 2009) and temperate (Wirth *et al.* 2009), sequester substantial amounts of carbon every year, and some of these are highly valuable for biodiversity.

We have assessed the synergies between climate mitigation and biodiversity conservation based solely on stocks of carbon and species. An important aspect missing from our analysis is that the conservation of these stocks is more relevant where their rate of loss might be greater (i.e., areas under higher risk of deforestation). In this sense, a further step to improve this assessment would be to analyze these synergies in a dynamic land-use change context.

A mechanism focused purely on carbon retention will not be optimal at conserving biodiversity, but there is much scope for improving the gains for biodiversity conservation, with low or no losses for carbon mitigation. Indeed, we found high variability in species counts across cells with similar biomass carbon levels (Figure 2). For instance, for total species richness there is approximately a five-fold difference in species richness per cell between the lower (red line, Figure 2A) and upper (blue line, Figure 2A) bounds of a 95% envelope. Cells in the upper bound usually have twice as many species as those expected by chance (mean, black line, Figure 2A). Taking biodiversity patterns into account when prioritizing areas for implementation could therefore substantially improve the contribution of REDD or similar mechanisms to global biodiversity conservation. This could be done by inserting a biodiversity premium for emissions from more biodiversity-rich areas directly into the REDD mechanism, by setting aside a fraction of REDD financing for targeting biodiversity-rich areas that would not be conserved for their carbon content alone (Strassburg *et al.* 2009), or by promoting cooperation between programs for REDD and conservation at a national to international scale, redirecting conservation funding to these areas (Grainger *et al.* 2009).

Climate change and biodiversity loss are two crises of global magnitude, each posing individual as well as synergistic risks to human well-being and curtailing humanity's future options (MEA 2005; Metz *et al.* 2007). Most of the world's governments have pledged both to reduce the rates of biodiversity loss (United Nations 1993) and to prevent dangerous climate change (United Nations 1992). Rather than addressing these two crises separately, it makes sense, where appropriate, to combine efforts and thereby achieve mutual gains. Our results confirm that mechanisms to reduce carbon emissions from deforestation and forest degradation will have side benefits in terms of biodiversity protection, as expected

given that forest conversion is a major driver of both climate change and biodiversity loss. Nonetheless, a purely carbon-focused mechanism does not necessarily focus on those forests where biodiversity conservation is most urgent, and attention should also be given to biodiverse areas outside the scope of proposed REDD mechanism that could become increasingly threatened. But our results suggest that if biodiversity distribution is taken into account, there might be substantial room for additional gains for biodiversity conservation without compromising the effectiveness of climate change mitigation. Our study confirms that the Parties to the United Nations Framework Convention on Climate Change have a singular opportunity to address two of the biggest challenges of our time, first and foremost by approving incentives for reducing carbon emissions from deforestation and forest degradation, and second by maximizing the potential of this mechanism to reduce rates of global biodiversity loss.

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Supporting Information

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

Table S1 Mean and range (min and max) of r_s coefficients and Dutilleul-corrected degrees of freedom (all coefficients have, $P < 0.01$)

Table S2 Summary statistics for the distribution of Spearman's Rank coefficients for noncorrelated cells (RCH = species richness; THR = threatened species; RST = restricted-range species)

Table S3 Generalized least squares (GLS) spatial models—parameter coefficients for biomass carbon (log-transformed) ($P < 0.0001$ in all cases)

Figure S1 Global biodiversity patterns based on the distribution of birds, mammals, and amphibians: (A) richness index, number of species per cell (out of 20,697 species); (B) threat index, number of threatened species per cell (out of 4,020 threatened species); (C) restricted range index, number of restricted-range species per cell (out of 5,248 restricted-range species).

Figure S2 Global distribution of above- and below-ground biomass carbon. Values per cell are the average carbon biomass per hectare of land area.

Figure S3 Global distribution of carbon in the top 100 cm of soil. Values per cell are the average soil carbon of land area.

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