

Research Article

The dangers of carbon-centric conservation for biodiversity: a case study in the Andes

Alvaro Duque^{1*}, Kenneth J. Feeley^{2,3}, Edersson Cabrera⁴, Ricardo Callejas⁵ and Alvaro Idarraga⁵

¹Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Calle 59A No. 63 - 20, Medellín, Colombia.

²Department of Biological Sciences, Florida International University, Miami, FL USA 33199

³Fairchild Tropical Botanic Garden, Coral Gables, FL USA 33156

⁴Instituto de Hidrología, Metreología y Estudios Ambientales –IDEAM, Carrera 10 No. 20-30 Of. 802, Bogotá, Colombia.

⁵Instituto de Biología – Herbario Universidad de Antioquia, Universidad de Antioquia. Cra 58 # 41 -36. Medellín, Colombia.

*Correspondence to: Alvaro Duque (ajduque09@gmail.com/ ajduque@unal.edu.co)

Abstract

Carbon-centric conservation strategies such as the United Nation's program to Reduce CO₂ Emissions from Deforestation and Degradation (REDD+), are expected to simultaneously reduce net global CO₂ emissions and mitigate species extinctions in regions with high endemism and diversity, such as the Tropical Andes Biodiversity Hotspot. Using data from the northern Andes, we show, however, that carbon-focused conservation strategies may potentially lead to increased risks of species extinctions if there is displacement (i.e., "leakage") of land-use changes from forests with large aboveground biomass stocks but relatively poor species richness and low levels of endemism, to forests with lower biomass stocks but higher species richness and endemism, as are found in the Andean highlands (especially low-biomass non-tree growth forms such as herbs and epiphytes that are often overlooked in biological inventories). We conclude that despite the considerable potential benefits of REDD+ and other carbon-centric conservation strategies, there is still a need to develop mechanisms to safeguard against possible negative effects on biodiversity in situations where carbon stocks do not covary positively with species diversity and endemism.

Keywords: forest conservation, deforestation, endemism, epiphytes, land-use change.

Resumen

Estrategias de conservación de bosques centradas en los contenidos de carbono, tales como el programa establecido por las Naciones Unidas para Reducir las Emisiones de CO₂ por Deforestación y Degradación (REDD+), se espera que ayuden simultáneamente a reducir las emisiones globales netas de CO₂ y la extinción de especies en regiones con alto endemismo y diversidad como los Andes tropicales. Sin embargo, con base en datos provenientes de la región norte de los Andes, aquí se muestra como las estrategias de conservación que se basan en la conservación del carbono, pueden potencialmente incrementar el riesgo de extinción de especies si hay desplazamiento de los cambios de uso del suelo de bosques con altos contenidos de biomasa aérea pero bajos niveles de riqueza de especies y endemismo (especialmente de las formas no arbóreas con baja biomasa que son poco tenidos en cuenta en los inventarios biológicos), como es el caso de los bosques de tierras altas en los Andes. Se concluye que, a pesar de los muy considerables beneficios potenciales de REDD+ y otros programas tipo-REDD, existe aún la necesidad de desarrollar mecanismos que ayuden a salvaguardar este tipo de estrategias de conservación contra posibles efectos negativos sobre la biodiversidad en aquellos casos en los que las reservas de carbono no covarían positivamente con la diversidad y el endemismo de especies.

Palabras claves: conservación de bosques, deforestación, endemismo, epifitas, cambio de uso del suelo.

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Introduction

Programs to Reduce CO₂ Emissions from Deforestation and Degradation (REDD+) have rapidly increased in prominence and have been widely touted as having the potential dual benefits of reducing carbon emissions (and hence rates of global climate change) and promoting species conservation through reductions in habitat loss. However, it remains unclear how effective REDD+ and other similar programs will be at reducing rates of species loss and extinction [1, 2]. Indeed, since the carbon stocks and species richness of forests are not equally distributed across the world [3], “carbon-centric” conservation programs, such as REDD+, that are based foremost on avoiding CO₂ emissions from deforestation, could actually increase rates of species loss. This is because of “leakage” whereby habitat loss and degradation are displaced from carbon-rich forests to other forests or ecosystems with low carbon contents but with potentially high levels of species richness and endemism [4-6]. In order to maximize the conservation of biodiversity while diminishing carbon emissions from deforestation, it will therefore be necessary to balance the potential co-benefits between carbon-centric policies [7] and diversity-focused strategies, such as the Convention for Biological Diversity (CBD) [8].

Carbon-centric conservation programs typically value tropical forests on the basis of their estimated aboveground woody biomass (AGB), which is used as a surrogate for an ecosystem’s total carbon content [9]. Therefore, under a purely carbon-focused strategy of conservation, forests with a low AGB but high species richness will receive lower prioritization for protection than forests with high AGB but low species richness [1]. In mountainous ecosystems, for example, the AGB stocks of forests typically decrease with elevation as a response to energy availability [10]. Lowland forests would therefore receive greater support for protection under carbon-centric conservation strategies than would highland forests that have lower AGB. This prioritization of lowland forests is reinforced by the fact that they tend to be more prone to deforestation due to greater access and lower slopes [11], as well as by the widespread, but often erroneous, belief that lowland ecosystems support more species than highland ecosystems [12]. The idea that lowland forests support more species than do the highlands has arisen at least in part because most research and surveys focus exclusively on the dominant or charismatic growth forms, such as trees and mammals [i.e. 13]. In reality, many growth forms and taxonomic groups, such as epiphytes, achieve their maximum diversity and abundance at mid to high elevations [14,15]. In other words, in mountainous ecosystems, total species richness or diversity may not covary positively and linearly with AGB. Carbon-centric protection strategies that favor high-biomass lowland forests may therefore have unintentional negative consequences for species conservation by displacing land conversion to more diverse but lower-AGB highland ecosystems.

The lack of a global consensus at the country level to value and curb CO₂ emissions has triggered the implementation of many project-based, local and subnational, voluntary initiatives [16], which could increase the risk of displacing land-use pressures to low-AGB systems with undesired consequences on biodiversity and ecosystem services [4]. Whereas the techniques to quantify biomass/carbon stocks in tropical forests have significantly improved over the last several years [17,18], the methods for evaluating biodiversity and cultural benefits associated with carbon maintenance and sequestration in natural ecosystems remain mostly unexplored [19]. The potential negative impacts of carbon-based conservation projects on either diversity or governance through leakage have been largely considered from a theoretical perspective [20]. More empirical examples [i.e. 6, 21] are needed in order to ameliorate and identify potential conflicts between biological and social targets .

To illustrate the potential risks to biodiversity posed by carbon-centric conservation strategies we estimated the risk of extinction within different growth forms of vascular plant species in relation to extent of habitat loss and rates of carbon release under alternative deforestation scenarios in the province of Antioquia, Northwest Colombia. In particular, we show the need to demonstrate the potential risk from the implementation of carbon-centric programs on the non-tree and other non-dominant growth forms in areas such as the tropical Andes, where diversity and endemism do not necessarily covary positively with AGB. The aim of this study is to inform researchers and organizations that focus on tropical ecology and forest conservation about the need to consider multiple life forms in designing conservation strategies. The results will also hopefully convince policy that there is the need to implement safeguard programs within REDD+ and other carbon-centric conservation programs in order to minimize their potentially negative effects on biodiversity.

Methods

Study area

The study was conducted in the province of Antioquia in northwest Colombia. Antioquia is located between 5°25' and 8°55' North and 7°53' and 77°07' West (Fig. 1), has an extent of approximately 63,108 km², and spans an elevational range of 0 (sea level) to 4,000 m asl. The province is mainly composed of the tails of the central and western Andean mountain ranges, but also contains some areas representing both the Caribbean and the Choco-Darien biogeographic regions. Annual precipitation in the region ranges from 1,000 mm to almost 7,000 mm. The topography and geology in the region are highly variable because of the presence of two mountain ranges influencing patterns of drainage, rainfall and soil fertility. Since the 18th century, most urban areas and settlements were located in the Central Cordillera, and the mountains in this portion of the region have suffered from intensive deforestation and fragmentation.

Floristic data

Species composition and endemism of vascular plants for the entire region, including both the lowlands (< 1500 m asl) and the highlands (> 1500 m asl) [22], were obtained from the Catalogue of Vascular Plants of Antioquia [23; see also <http://www.tropicos.org/Project/CV>], which exactly overlaps the study region. The Catalogue is the first and only work describing in detail the flora of an entire region within Colombia. Before running the analyses, we excluded all introduced species as well as all species that were found only in the Paramos (non-forested grassland habitats occurring above the alpine treeline). We divided all remaining plant species into six growth forms: 1) trees (including shrubs), 2) epiphytes (including hemi and holo-epiphytes), 3) herbs, 4) lianas (including woody and non-woody vines), 5) parasites, and 6)

saprophytes. For the entire region, plant endemism (%) was calculated as the proportion of species within each life form that have only ever been recorded within the geographic boundaries of the Antioquia province (i.e., global endemics to Antioquia). In identifying and tallying the number of endemics, we classified them as being highland specialists (i.e., those occurring exclusively above 1,500 m asl), lowlands specialists (i.e., those occurring exclusively below 1,500 m asl) or elevational generalists (occurring both above and below 1,500m asl).

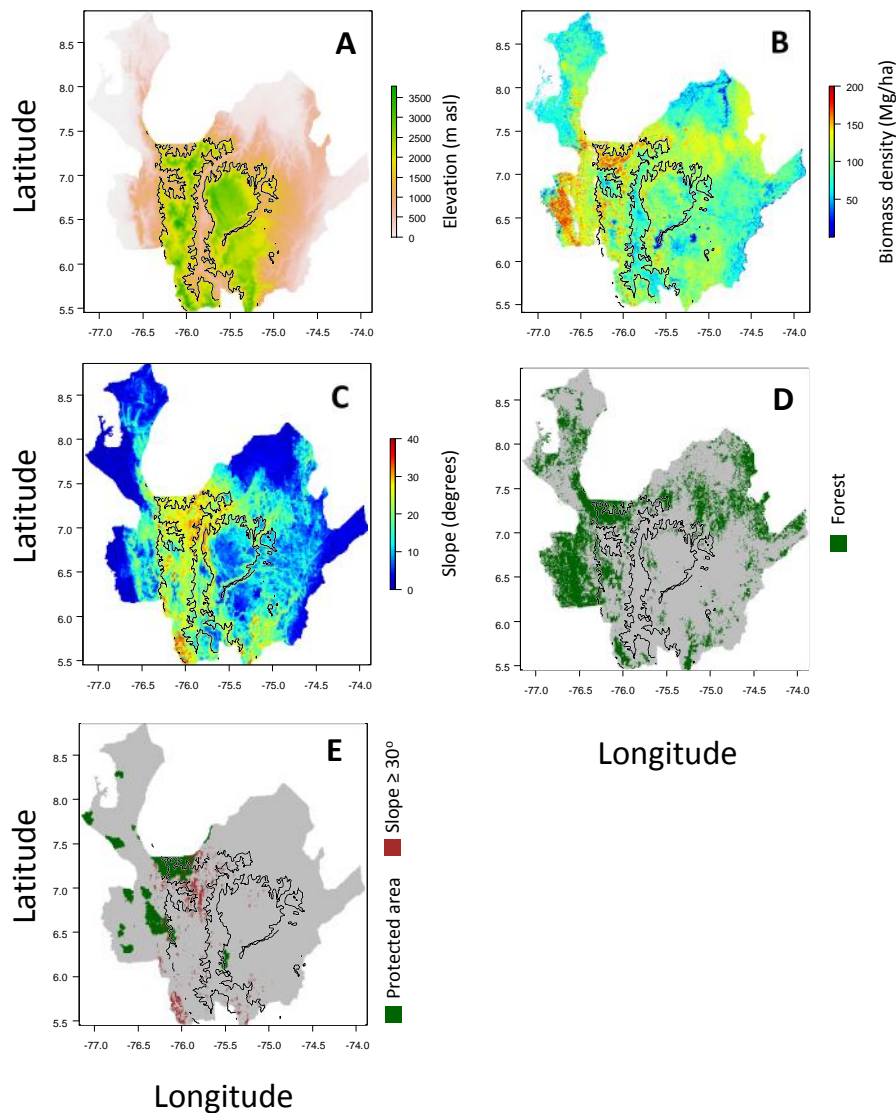


Fig. 1. Panels A, B and C depict the elevation, estimated aboveground biomass, and slope, respectively, in Antioquia province, Colombia. Panels D and E respectively indicate areas that are classified as having forest cover and areas that were excluded from deforestation models due to being either legally protected or having steep terrain (slope $\geq 30^\circ$). In all panels, the 1500 m elevation contour line separating the highlands from the lowlands is shown.

Carbon loss by deforestation

Forested areas within Antioquia province were mapped using a 2010 Landsat image with a spatial resolution of 30m (ETM+ and TM sensors). Digital image processing and mapping of the forest cover was carried out using a semi-automated approach that integrates the CLASlite software (www.claslite.ciw.edu) and expert criteria. The topography (elevation and slope) of the forested areas of Antioquia were mapped using the SRTM Digital Elevation Model (DEM, <http://srtm.csi.cgiar.org/>) with 90m spatial resolution. The approximate distribution of estimated aboveground biomass (AGB) in the forests of Antioquia was mapped at a spatial resolution of 30 arc seconds (approximately 1 km²), according to Saatchi et al [18]. All maps were rescaled to a matching spatial resolution of 30 arc seconds (Fig. 1).

Based on the maps described above, three different simplified scenarios of deforestation were simulated: 1) Business-As-Usual (BAU), which assumes that the order in which different areas (pixels) are deforested will be determined by their slope such that the flattest areas (i.e., with lowest slopes) are deforested first; 2) Carbon-Centric Protection (CCP), which assumes that areas with high AGB will receive greater protection and consequently the order in which sites are deforested will go from low to high AGB; and 3) a Worst-Case Scenario (WCS – from the carbon-centric viewpoint), which assumes that the order in which areas are deforested is in direct relation to their AGB with high AGB forests being cleared first. In all scenarios, areas with slopes $\geq 30\%$ or within protected areas were considered exempt from deforestation (8.3% and 0.4% of lowland forest are within protected areas and/or have steep slopes, respectively; 9.8% and 36.0% of highland forests are within protected areas and/or have steep slopes, respectively; Fig. 1). It is important to note that these simulations do not incorporate any assumptions about either the drivers or the actual rates of deforestation, but rather are simplified predictions of the order in which different areas will be deforested [see 11]. The simulation scenarios therefore allow us to look at the relationships between species extinction risks, carbon emissions, and total extent of deforestation independent of time.

Carbon emissions

We estimated the amount of carbon emitted (MT) per km² of deforestation under each of the three deforestation scenarios described above by assuming that deforestation results in 100% of the above-ground carbon being emitted and that AGB is 50% carbon [9].

Species loss and extinction

We predicted the number of plant species that will go extinct, or become committed to extinction, per km² of deforestation under each of the three simulation scenarios by applying the principles of island biogeography theory. According to the island biogeography theory, the number of species in a habitat is related to the area of habitat through the power function $S = cA^z$, where S is the number of species, A is habitat area and c and z are constants. The proportion of species that will eventually be lost due to deforestation (SL) can be estimated by

$$SL = S_0 - S_n (A_n / A_0)^z$$

where S_0 and A_0 are the initial number of species and the initial area, and S_n and A_n are the number of species and the area post deforestation [24, 25]. In estimating species extinction rates, we assumed that all of the highland species occur throughout the highlands and likewise that all lowland species occur throughout the lowlands. We then estimated habitat loss for each of the different highland and lowland life forms by calculating the percent habitat remaining (A_n / A_0) in the highlands and lowlands, respectively, per extent of total deforestation as predicted under the three alternative deforestation scenarios. We estimated the number of species that will go extinct as the proportional species loss (SL) multiplied by the number of (global) endemic plant species. For this analysis we just used the endemic species classified as

being specialist in the lowland and highland forests to calculate the number of species that will go extinct (i.e., we did not consider the possible extinction of elevation generalist species as this should not vary between the deforestation scenarios). In our calculations, we assumed $z = 0.25$ because this value is well-supported by empirical studies and allows for cross-comparisons with previous studies [24-26]. The use of island biogeography theory in estimating rates of species loss has been heavily debated in the literature [27], but it remains a common practice in conservation planning and risk assessment, particularly in the absence of detailed information on the relative abundances of species and their spatially explicit distributions.

Results

Aboveground biomass, species richness, and species endemism.

In 2010, highland forests accounted for 8.3% and lowlands forests accounted for 20.9% of Antioquia province, which had an original cover of 28.8% highland and 71.2% lowland forests. The mean estimated-AGB of forests in the Antioquia province was 208.5 Mg ha^{-1} . As expected, the AGB was markedly higher in lowland vs. highland forests (216.1 vs. 183.2 Mg ha^{-1}) (Fig. 2).

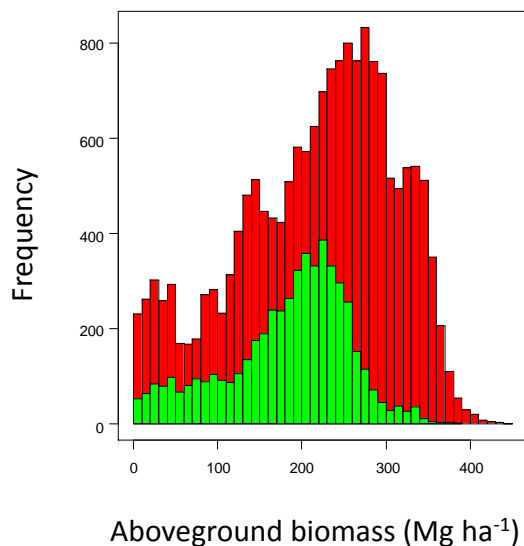


Fig. 2. The distribution of aboveground biomass density in lowland (red) and highland (green) forests of Antioquia province, Colombia.

To date, a total of 7,664 native vascular plant species have been collected and identified in Antioquia province. The lowlands have greater total species richness than do the highlands. The growth form with the greatest total species richness was “trees and shrubs”, which represented 37.4% of the total plant species richness. In contrast, the growth form with the lowest species richness was “saprophytes” which represented just 0.2% of the total plant species richness. In the lowland forests, “trees and shrubs” constituted the richest growth form (1,598 spp); in the highlands, “herbs” were the richest growth form (963 spp; Table 1A).

There were 580 plant species that are globally endemic to the region. “Epiphytes” were the growth form with the highest total number of endemic species (18.7%). There were no endemic “saprophytes”. In the lowlands, “trees and shrubs” had the highest number of endemic species (63). In the highlands, “epiphytes” had the highest number of endemic species (194; Table 1B).

Table 1. Number of native and endemic species of vascular plants recorded in the Antioquia province

Growth form	Lowlands (0-1,500 masl)	Highlands (1500-4000 masl)	Number of shared species	No elevation data	Total
A. All data					
Trees and shrubs	1,598	731	548	4	2,881
Epiphytes	363	840	225	22	1,450
Herbs	952	963	497	6	2,418
Lianas	507	172	137	4	820
Saprophytes	9	5	1	0	15
Parasites	28	36	16	0	80
Total	3,457	2,747	1,424	36	7,664
B. Endemics					
Trees and shrubs	63	67	27	1	158
Epiphytes	38	194	17	9	258
Herbs	48	73	8	1	130
Lianas	8	10	5	0	23
Saprophytes	0	0	0	0	0
Parasites	4	5	1	0	10
Non-data	0	0	1	0	1
Total	161	349	59	11	580

Effect of carbon-centric conservation on species extinctions risks

The three different scenarios of deforestation led to contrasting patterns of forest loss between lowlands and highlands (Fig. 3). A carbon-centric forest protection strategy in which priority for protection is based solely on estimated-AGB has the potential to markedly reduce carbon emissions from the Antioquia province, even if the rate or extent of total deforestation does not change (Fig. 4). This potential reduction in carbon emissions per extent of deforestation is due to a shift in deforestation away from the high-AGB lowlands to the low-AGB highlands. Given the resultant increase in deforestation in the low-biomass highland areas and the high proportion of endemic species that inhabit these montane forests, we predict that a carbon-centric strategy that does not markedly reduce the total extent of deforestation could therefore actually have an overall negative effect on species diversity (Fig. 5). The potential negative

effects of carbon-centric conservation strategies are greatly magnified in the non-tree life forms, which have elevated levels of endemic diversity in highlands (Fig. 6). In particular, the extinction risk of epiphytes dramatically increases under our CCP vs. non-CCP deforestation scenarios due to the high diversity and endemism of species in this life form in the low-AGB forests found above 1,500m elevation (Fig. 6).

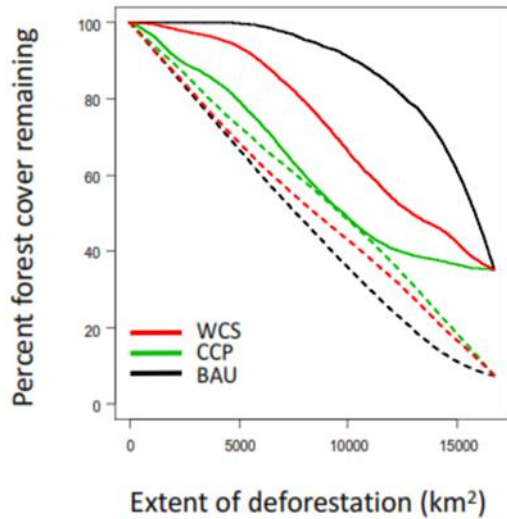


Fig. 3. The percent of forest cover remaining in the lowlands (elevation <1,500 m asl; solid lines) and highlands (elevation ≥1,500m asl; dashed lines) following different total amounts of deforestation under three different deforestation scenarios: BAU = Business-As-Usual, which assumes that flat areas are deforested first; CCP = Carbon-Centric Protection, which assumes that low biomass areas will be deforested first; WCS = a Worst-Case Scenario (from the carbon-centric viewpoint), which assumes that high biomass areas will be deforested first. Percent forest cover remaining does not reach 0% since in all scenarios, areas with slopes ≥30% or within protected areas were considered exempt from deforestation (8.3% and 0.4% of lowland forest are within protected areas and/or have steep slopes, respectively; 9.8% and 36.0% of highland forests are within protected areas and/or have steep slopes, respectively).

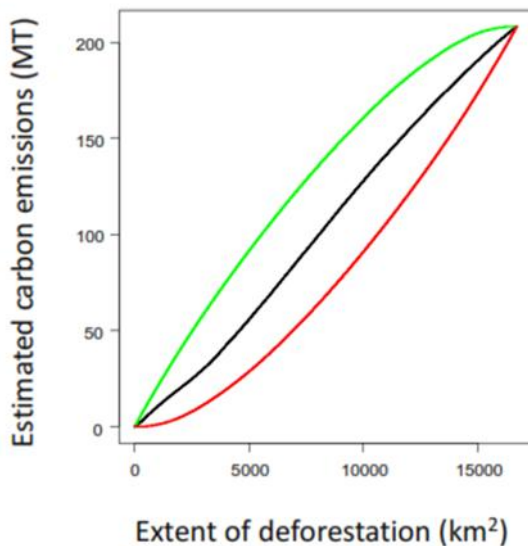


Fig. 4. Estimates of carbon emissions due to different total amounts of deforestation under three different deforestation scenarios: BAU = Business-As-Usual, which assumes that flat areas are deforested first; CCP = Carbon-Centric Protection, which assumes that low biomass areas will be deforested first; WCS = a Worst-Case Scenario (from the carbon-centric viewpoint), which assumes that high biomass areas will be deforested first.

Discussion

The need to balance carbon-centric with diversity-focused policies to minimize species extinctions

In this case study, we show that applying the principles of carbon-centric protection strategies in the province of Antioquia can have positive effects on reducing CO₂ emissions due to deforestation, but may have negative effects on species diversity by increasing extinction risk of endemic species, especially of non-tree growth forms such as epiphytes. These conclusions are likely to hold for areas outside of Antioquia and even for areas outside of the Andes. Indeed, carbon-centric conservation strategies have the potential to increase risks of species extinctions in any areas where there is not a strong congruence between estimated-AGB stocks and species diversity. The Amazonian white-sand forest and the Atlantic Forest of South America [7] as well as the lowland mineral-soil forests of Indonesia [6], which have well known incongruences between carbon stocks and species richness, are good examples of areas with high potential risk of species extinction if carbon-centric strategies are applied. Our results suggest that the co-benefits of REDD+ and other carbon-centric programs for the conservation of biodiversity in tropical forests will largely depend on the fine-scale relationships among deforestation, carbon stocks, and species richness [2], rather than on the global relationships between carbon stocks and species richness highlighted in most recent studies [1,3,13]. These findings highlight the potential perils of focusing priorities on a single conservation metric (i.e., reducing carbon emissions) in policies meant to mitigate climate change [8].

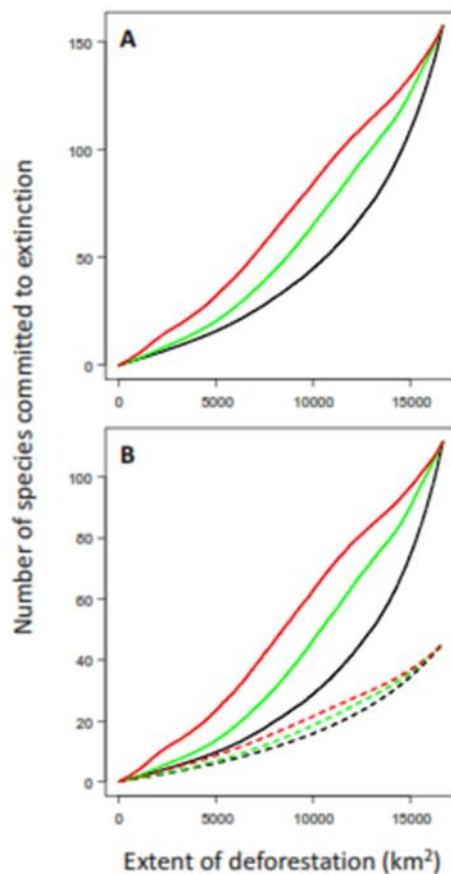


Fig. 5. The A) total number of endemic plant species and B) number of non-tree (solid lines) vs. tree (dashed lines) species estimated to become committed to extinction due to different total amounts of deforestation under three different deforestation scenarios: Black = Business-As-Usual (BAU), which assumes that flat areas are deforested first; Green = Carbon-Centric Protection (CCP), which assumes that low biomass areas will be deforested first; Red = a Worst-Case Scenario (WCS – from the carbon-centric viewpoint), which assumes that high biomass areas will be deforested first.

Diversity of dominant forms as surrogate of the total species diversity

Our results do not support the use of tree species richness as a surrogate of overall species richness. The incongruence between tree diversity and the diversity of other plant life forms, for example epiphytes, has been previously reported in different landscape units in the Amazon basin [28]. Nonetheless, many forest conservation strategies use tree diversity as the primary, if not sole, measure of species richness [9]. This focus is due in part to the fact that trees are the most conspicuous elements of the forest and provide habitat, food, and shelter for many other organisms. However, trees commonly represent less than half of the vascular plant species occurring in tropical forests [23,29], which in many cases could hamper the effectiveness of planning for the conservation of biodiversity through tree-focused programs. The use of the diversity patterns of dominant or charismatic growth forms (e.g., trees and large mammals) as surrogates for other growth forms (e.g., epiphytes and small amphibians), could leave many known and unknown species unprotected, thereby inadvertently increasing their extinction risk and the potential for greater rates of overall species loss [30].

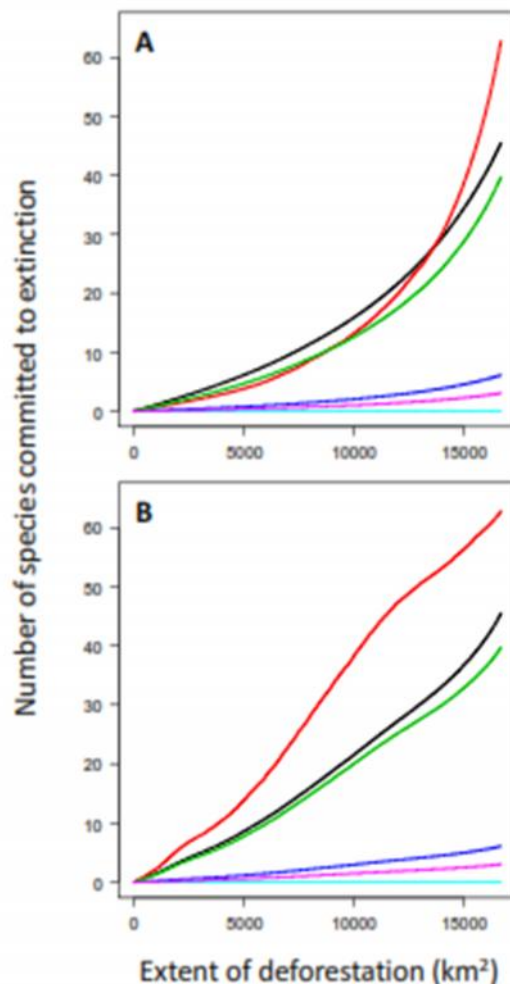


Fig. 6. The number of endemic plant species of different life forms that are estimated to become committed to extinction due to different total amounts of deforestation under A) a Business-As-Usual (BAU) deforestation scenario and B) a Carbon-Centric Protection (CCP) deforestation scenario. Black = trees, red = epiphytes, green = herbs, blue = lianas, magenta = parasites, and turquoise = saprophytes.

The “carbonization” of the agenda for forest conservation

Despite the uncertainty about the long-term capability of forests for storing and sequestering carbon in the face of global warming [31,32], curtailing CO₂ emissions from deforestation would offset a sizable portion of the excess of greenhouse-gas emissions from industrialized countries [9]. This fact, combined with a desire to decrease rates of climate change, has “carbonized” the international conservation agenda, increasing the attention on REDD+ and other carbon-centric strategies while marginalizing the needs for biodiversity (and other ecosystem services) protection. Therefore, additionality and opportunity costs may play an important role in determining the carbon market. In the case of additionality, in mountainous ecosystems the functionality in terms of multiple services (e.g., watershed protection) could be counted as part of the economic benefits [33]. Epiphyte diversity and abundance could also be used as indicators for monitoring water storage and regulation [34], which in our study region is highly linked to hydro-power generation. In many forested areas that are under threat of conversion, the opportunity costs of infrastructure projects, such as new roads and dams, could make the carbon market non-competitive. In the Antioquia province, the development of new roads has promoted the rapid conversion of forests to grasslands independent of the need to increase pasture lands. In many cases, the conversion of forests to grasslands is accelerated by local people’s often-erroneous association of forests with poverty and grasslands with improved livelihoods. Furthermore, due to the social characteristics of the study region, new roads and land conversion have also triggered social inequalities and population displacement to the largest cities, which are mostly located in the highlands. Hence, to avoid deforestation, diversity loss, and species extinction, we need to mix the potential economic opportunities and incentives offered by carbon-centric programs with more complex strategies that take into account species distributions of multiple life forms and the functionality of the ecosystems, as well as the cultural and social realities of the target regions [19].

Implications and conservation

Given that a major rationale for curbing anthropogenic-mediated global climate change is to preserve and maintain species diversity, conservation programs must explicitly incorporate values of species diversity into policies and practices. The potential congruence between carbon stocks and species richness reported at a global scale in some studies designed to maximize the co-benefits of reducing deforestation on species diversity [1,3,7] will in many cases need to be re-evaluated before implementing REDD+ and REDD-like programs at subnational and local scales. Problems associated with the generalized and often-erroneous assumption of a lower species diversity in low-AGB ecosystems will always need to be assessed through extensive local and regional surveys and censuses. Non-critical acceptance of such erroneous assumptions could indirectly promote the displacement of deforestation and the likelihood of species extinctions to unprotected, low-carbon but high-diversity habitats such as the tropical Andes.

We stress that the intent of this study is not to deny the utility of REDD+ or other carbon-centric programs for conservation. We recognize that curtailing deforestation is a necessary step towards mitigating species loss and carbon emissions. However, the need to balance the payments for forest conservation with principles of complementarity that include diversity-focused policies is paramount. We also stress that any successful policy must aim to safeguard hotspots and localized endemic species (including species of non-tree life forms) that are not typically included in the carbon-centric strategies.

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References

- [1] Venter, O., Laurance, W.F., Iwamura T, Wilson, K.A., Fuller, R.A. and Possingham, H.P. 2009. Harnessing carbon payments to protect biodiversity. *Science* 326:1368.
- [2] Strassburg, B., Rodrigues, A., Gusti, M., Balmford, A., Fritz, S., Obersteiner, M., Turner, R.K. and Brooks, T.M. 2012. Impacts of incentives to reduce emissions from deforestation on global species extinctions. *Nature Climate Change* 2:350-355.
- [3] Thomas, C.D., Anderson, B.J., Moilanen, A., Eigenbrod, F., Heinemeyer, A., Quaife, T., Roy, D.B., Gillings, S., Armsworth, P.R. and Gaston, K.J.. 2013. Reconciling biodiversity and carbon conservation. *Ecology Letters* 16:39-47.
- [4] Miles, L. and Kapos, V. 2008. Reducing greenhouse gas emissions from deforestation and forest degradation: global land-use implications. *Science* 320:1454-1455.
- [5] Gardner, T.A., Burgess, N.D., Aguilar-Amuchastegui, N., Barlow, J., Berenguer, E., Clements, T., Danielsen, F., Ferreira, J., Foden, W., Kapos, V., Khan, S.M., Lees, A.C., Parry, L., Roman-Cuesta, R.M., Schmitt, C.B., Strange, N., Theilade, I., Vieira, I.C.G. 2012. A framework for integrating biodiversity concerns into national REDD++ programmes. *Biological Conservation* 154:61-71.
- [6] Harrison, M.E. and Paoli, G.D. 2012. Managing the risk of biodiversity leakage from prioritising REDD+ in the most carbon-rich forests: the case study of peat-swamp forests in Kalimantan, Indonesia. *Tropical Conservation Science* 5:426-433.
- [7] Strassburg, B., Kelly, A., Balmford, A., Davies, R.G., Gibbs, H.K., Lovett, A., Miles, L., Orme, C. D.L., Price, J., Turner, R.K., & Rodrigues, A.S.L. 2010. Global congruence of carbon storage and biodiversity in terrestrial ecosystems. *Conservation Letters* 3:98-105.
- [8] Siikamäki, J. and Newbold, S.C. 2012. Potential biodiversity benefits from international programs to reduce carbon emissions from deforestation. *Ambio* 41:78-89.
- [9] IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: synthesis report. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC.
- [10] Girardin, C.A.J., Malhi, Y., Aragao, L.E.O.C., Mamani, M., Huaraca-Huasco, W., Durand, L., Feeley, K.J., Rapp, J., Silva-Espejo, J.E., Silman, M., Salinas, N. And Whittaker, R.J. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology* 16: 3176–3192.
- [11] Sandel, B. and Svenning, J-C. (2013). Human impacts drive a global topographic signature in tree cover. *Nature Communications* 4 Available online. DOI:10.1038/ncomms3474
- [12] Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press.
- [13] Venter, O., Meijaard, E., Possingham, H., Dennis, R., Sheil, D., Wich, S., Hovani, L. and Wilson, K. 2009. Carbon payments as a safeguard for threatened tropical mammals. *Conservation Letters* 2:123:129.

- [14] Churchill, S.P. 1991. The floristic composition and elevational distribution of Colombian mosses. *The Bryologist* 94:157–167.
- [15] Kreft, H., Koster, N., Kuper, W., Nieder, J. And Whilhelm, B. 2004. Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuni, Ecuador. *Journal of Biogeography* 31:1463–1476.
- [16] Hurteau, M.D., Hungate, B.A., Koch, G.W., North, M.P. and Smith, G.R. 2013. Aligning ecology and markets in the forest carbon cycle. *Frontiers in Ecology and the Environment* 11: 37-42.
- [17] Asner, G.P., Powell, G.V.N., Mascaro, J., Knapp, D.E., Clark, J.K., Jacobson, J., Kennedy-Bowdoin, T., Balaji, A., Paez-Acosta, G., Victoria, E., Secada, L., Valqui, M. and Flint Hughes, R. 2010. High-resolution forest carbon stocks and emissions in the Amazon. *Proceedings of the National Academy of Sciences*. 107:16738-16742.
- [18] Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchar, E.T.A., Salas, W., Zutta, B.R., Buermann, S, Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M., and Morel, A. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Science*. 108:9899-9904.
- [19] Grabowski, Z.J. and Chazdon, R.L. 2012. Beyond carbon: redefining forests and people in the global ecosystem market. *SAPIENS*. 5:1-14.
- [20] Angelsen, A. (ed.) (2008) *Moving Ahead with REDD: Issues, Options and Implications*. CIFOR, Bogor.
- [21] Baker, T.R., Jones, J.P.G., Thompson, O.R., Cuesta, R.M.R., del Castillo, D., Chan, I., Torres, J. and Healey, J.R. 2010. How can ecologists help realise the potential of payments for carbon in tropical forest countries? *Journal of Applied Ecology* 47:1159–1169.
- [22] Gentry, A. 1995. Patterns of diversity and floristic composition in Neotropical Montane Forests. In: *Biodiversity and Conservation of Neotropical Montane Forests*. Churchill, S.P., Balslev, H., Forero, E. and Luteyn, J. (Eds.). pp. 103-126. The New York Botanical Garden, New York, EEUU.
- [23] Idárraga, A., Ortiz, R.C., Callejas, R. and Merello, M. 2011. *Flora de Antioquia: catálogo de las plantas vasculares. vol. II. Listado de las plantas vasculares del departamento de Antioquia*. Programa Expedición Antioquia-2103. Series Biodiversidad y Recursos Naturales. Universidad de Antioquia, Missouri Botanical Garden y Oficina de planeación departamental de la gobernación de Antioquia. Editorial D’Vinni, Bogotá, Colombia.
- [24] Pim, S.L. and Raven, P. 2000. Extinction by numbers. *Nature* 403:843-845.
- [25] Feeley, K.J. and Silman, M.R. 2009. Extinction risks of Amazonian plant species. *Proceedings of the National Academy of Science* 106:12382-12387.
- [26] Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. And Hilton-Taylor, C. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16: 909-923.
- [27] He, F. and Hubbell, S 2011. Species–area relationships always overestimate extinction rates from habitat loss. *Nature* 473:368-371.
- [28] Benavides, A.M., Duque, A., Duivenvoorden, J.F., Vasco, A. And Callejas, R. 2005. A first quantitative census of vascular epiphytes in rain forests of Colombian Amazonia. *Biodiversity and Conservation* 14:739–758.
- [29] Jørgensen, P.M. and León-Yáñez, S. (Eds). 1999. *Catalogue of the vascular plants of Ecuador*. Missouri Botanical Garden Press, St. Louis.
- [30] Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, A., Still, C.J. & Young, B.E. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161-167.

- [31] Gullinson, R.E., Frumhoff, P.C., Canadell, J.G., Field, C.B., Nepstad, D.C., Hayhoe, K., Avissar, R., Curran, L.M., Friedlingstein, P., Jones, C.D. and Nobre, C. 2007. Tropical Forests and Climate Policy. *Science* 316: 985-986.
- [32] Phillips, O.L., Aragão, L.E., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, A., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J. Alves de Oliveira, A.C., Dávila-Cardozo, N., Czimczik, C.I., Feldpausch, T.R., Freitas, M., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A. Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., ter Steege, H., Stropp, J., Vásquez, R., Zelazowski, P., Alvarez-Dávila, E., Andelman, S., Andrade, A., Chao, K-J, Erwin, T., Di Fiore, A., Honorio, E., Keeling, H., Killeen, T., Laurance, W.F., Peña-Cruz, A., Pitman, N.C.A., Núñez-Vargas, P., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J. and Torres-Lezama, A. 2009. Drought sensitivity of the Amazon rainforest. *Science* 323: 1344–1347.
- [33] Herrador, D. and Dimas, L. 2000. Payment for Environmental Services in El Salvador. *Mountain Research and Development* 20:306-309.
- [34] Sommerville, M.M., Milner-Gulland, E. J. and Julia PG Jones, J.P.G. 2010. The challenge of monitoring biodiversity in payment for environmental service interventions. *Biological Conservation* 144:2832-2841