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Short Communication

Enhancing ecosystem function through conservation: threatened plants increase local carbon storage in tropical dry forests

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Abstract
The role of plant diversity, particularly of rare species, in ecosystem functioning (*e.g.,* carbon storage) has been mostly studied in temperate systems with little practical application to the conservation of tropical forests, where species rarity and species richness tend to be greater and more important for ecosystem functioning. We linked carbon storage pools with functional plant diversity, occurrence of rare species, and environmental (topographic) gradients in a species-rich seasonally dry tropical forest protected as a part of a Biosphere Reserve in northwestern Mexico. We estimated various functional diversity and carbon pool measures from *in situ* plant community and soil data. Soil and total ecosystem carbon storage decreased with slope steepness but increased with plant height. Above-ground carbon was negatively associated with elevation. Our data suggest that species identity matters to the functioning and productivity of seasonally dry tropical forests. Two long-lived and highly threatened rare plant species contributed considerably (10-20%) to the above-ground carbon storage pool. The functional roles of threatened plant species should be investigated and incorporated into the management plans of Biospheres Reserves and other closely coupled natural-human systems, where conservation plays a significant role in ecosystem functioning and human well-being.

Keywords: carbon storage, ecosystem services, Man and Biosphere Program, REDD+ Program, seasonally dry tropical forests, natural protected areas

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Introduction

Tropical forests are well known not only for their high biodiversity and carbon pools, but also for their many endemic and rare species threatened by human population growth and economic development [1]. Seasonally dry tropical forests (SDTF) face threats typical of tropical forests worldwide, particularly land-use change [2, 3]. Seasonally dry tropical forests harbor numerous endemic and threatened plant species that may have unique combinations of functional traits. Globally rare or endangered plant species can be locally abundant and thus contribute significantly to ecosystem functions such as productivity at local or regional scales [4, 5]. A significant role in the ecosystem function (*e.g.*, increased carbon storage) may be an important argument for the conservation of threatened species beyond their traditional intrinsic value. Carbon storage is one of the most important forest ecosystem services, with positive or negative effects on global climate change, depending on whether ecosystems act as sinks or sources of carbon dioxide [6]. The two main terrestrial carbon pools are soil organic carbon and aboveground biomass carbon; together these two pools make up most of the total ecosystem carbon in SDTF. By linking carbon storage pools with functional diversity, we improve biodiversity conservation because related ecosystem services (*e.g.,* plant productivity or erosion control) can directly influence human land-use and ultimately human welfare.

In SDTF systems, in addition to the seasonal precipitation that affects species' leaf habit (*e.g.,* deciduous *vs*. evergreen) and thus functional diversity, topography may strongly affect biomass accumulation and carbon storage pools by influencing the availability of key plant resources such as light, water and nutrients [7, 8, 9]. Our objective was to study the linkages among carbon storage pools, topography, functional diversity, and threatened species in a protected, species-rich, seasonally dry tropical forest. Our study is located in a Biosphere Reserve of the Man and Biosphere Program (MAB) of United Nations, directly meeting the main goal of this global program to support biodiversity conservation and sustainable use of natural resources by local communities. At the same time, our study matches the goals of another United Nations initiative (REDD+: Reducing Emissions from Deforestation and Forest Degradation), which embraces the role of conservation and management to enhance forest carbon stocks in developing countries.

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Methods

Study area and site selection

The study sites are located in the Sierra de Alamos-Rio Cuchujaqui Biosphere Reserve, a 93,000 ha protected area located at 27°12' to 26°53' N, 109°03' to 108°29' W at the northern range limit of Neotropical SDTF in northwestern Mexico (Fig. 1). Agroforestry is widespread and is the main economic activity for local people within and outside the Biosphere Reserve. The climate is warm and semi-arid with annual precipitation of 712 mm and temperature of 24 ºC. The dry season is from November to May, and the rainy season from June to October, when ~80 % of the annual precipitation occurs [10].

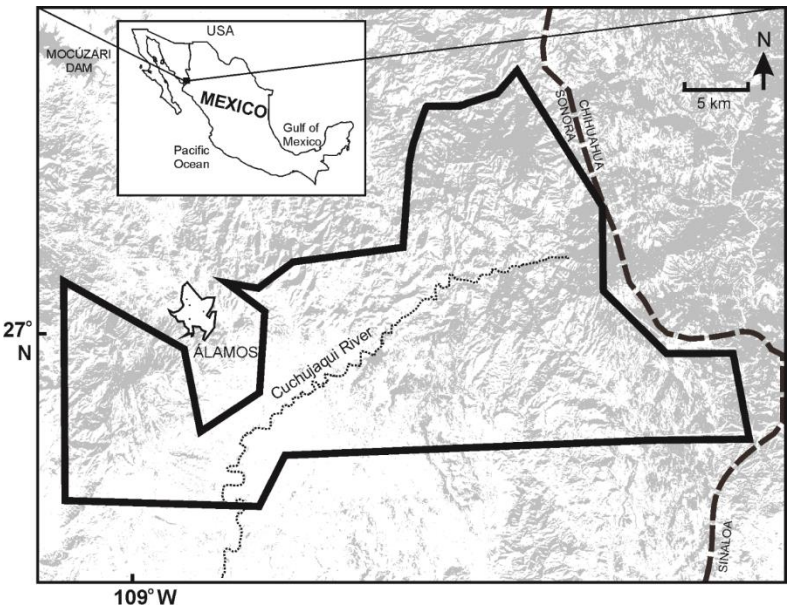


Fig. 1. Location of the study area, the Biosphere Reserve Sierra de Alamos - Rio Cuchujaqui (irregular shaped polygon) in the state of Sonora in northwestern Mexico.



Fig. 2. Photographs showing the seasonally dry tropical forest of the Biosphere Reserve Sierra de Alamos-Rio Cuchujaqui in northwestern Mexico (a), the cycad *Dioon sonorense* (b), and the palm *Brahea aculeata* (c). Photo credit: J.C. Álvarez-Yépiz.

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Elevation in the Biosphere Reserve ranges from 300 to 1,800 m above sea level (asl). Elevation and slope steepness are the main environmental gradients structuring the community composition in the Biosphere Reserve, with high elevations characterized by poor soil fertility and lower elevations by higher soil fertility [7, 10]. These gradients also seem important for the distribution of the rare endangered cycad *Dioon sonorense* (De Luca, Sabato and Vazq.Torres) and the threatened endemic palm *Brahea aculeata* (Brandegee) Moore, which co-occur within the Biosphere Reserve roughly between 500 and 1,000 m asl [7]. In this elevation range, we established 27 plots (three 20 × 20 m plots in each of the nine different study sites) to characterize community composition and the environment. Plot location corresponded to the population distribution of the rare cycad *D. sonorense* and the threatened palm *B. aculeata,* since we were interested in their potential contribution to local carbon storage (Fig. 2).

Estimating carbon pools

In order to estimate standing biomass, we characterized community structure and composition by identifying all shrub and tree species and measuring their height (m) and diameter at breast height (DBH; measured at 1.30 m height for all stems with DBH ≥2 cm). We measured 1,088 individuals from 56 species in all plots. Because *D. sonorense* is a short understory species, we measured basal diameter instead of DBH for all adult individuals (plants ≥ 100 cm tall, [7]). Above-ground dry biomass was estimated using an allometric equation based on individual tree basal areas, which was developed for SDTFs [11] and successfully used in our study region [10]. Because the allometric equation did not originally include understory cycad or palm species, and to avoid any artifacts of biomass estimation on our final models for carbon storage, we estimated biomass of the cycad and palm species using two different approaches: a general formula developed for the main SDTF species [11], and a more specific formula developed for species with palm-like growth form [12]. The final (best) models for predicting carbon storage contained the same predictors regardless of the equation used. Due to the similarity in growth forms of palms and cycads (compared to the other species present), we report results using the estimations derived from the equation for palm-like growth forms [12]. Because this study included federally listed threatened plant species (cycad and palm species) protected as part of the Biosphere Reserve conservation plan, we were not able to directly measure biomass by harvesting plants, but our models offer insight on the importance of protected threatened species in a Biosphere Reserve dominated by the STDF ecosystem.

We converted the total above-ground biomass value per plot to above-ground carbon (AGC) employing a widely used conversion factor (biomass × 0.5) [13]. Soil organic carbon (SOC) pools were obtained for each plot by multiplying (*i*) organic carbon content (g kg^{-1}), (*ii*) soil bulk density (g cm^{-3}), and (*iii*) a conservative depth value of 20 cm (to avoid overestimation of SOC on shallow soils). Bulk density was obtained by the paraffin method and organic carbon content by the Walkley–Black method in three composite soil samples per site (additional details in [7]). Total ecosystem carbon (TEC) was estimated by adding AGC and SOC. In order to avoid pseudoreplication we averaged plot values per site. All carbon pools were expressed in Mg C ha^{-1}.

Measuring functional diversity

As recommended for trait-based field studies [14, 15], we selected the most abundant species (in this case accounting for 50-90% of total relative abundance on each site) for our estimation of several functional diversity indices at each site. We measured individual plant height (m) and leaf

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nitrogen content (N, %), and carbon stable isotope ratio ($\delta^{13}C$, ‰, a proxy positively related to water-use efficiency –WUE), following standard procedures for processing and analyzing leaf samples (three samples of 2.5-3.0 mg for each species with >50% relative abundance; see [8] for additional details). We used the FD package to calculate single-trait (CWM) and multi-trait functional diversity estimates [16]. We calculated community-weighted means of height (CWM.H), leaf N content (CWM.N) and $\delta^{13}C$ (CWM. $\delta^{13}C$). Our multi-trait index of functional divergence denoted as FDiv (calculated using height, leaf N and $\delta^{13}C$) was highly positively correlated with two other commonly used multi-trait diversity indices (RaoQ, Pearson r= 0.65, and functional dispersion, Pearson r= 0.72). We only report FDiv, which is closely related to niche differentiation through complementarity; it varies from 0 to 1 and is largest when functionally different species reach similarly high abundances [17].

Data analysis

We calculated mean site values (*i.e.*, we averaged three field plots per site, for the total *N*=9) for the single and multi-trait functional diversity components (CWM. H, CWM.N, CWM.$\delta^{13}C$, and FDiv), three carbon pools (AGC, SOC, and TEC), and two topographic variables (elevation and slope steepness). We used a general linear modeling framework to relate each carbon storage pool (AGC, SOC, TEC) to both the functional diversity components and the two topographic gradients. In order to reduce Type I error, only significantly correlated predictors with at least one of the carbon storage components were included in the models. The best model for each carbon pool was the one that minimized the Akaike's Information Criterion (AIC) in the stepwise (forward) model selection. We used the leave-one-out cross-validation (LOOCV) technique to estimate prediction error, an important consideration for smaller datasets. Our best models consistently had the lowest prediction error (LOOCV) and explained the highest variance (R^2) relative to all other models. We specifically tested the effects of threatened species (the cycad *D. sonorense* and the palm *B. aculeata*) by including their abundance (density per site) as an additional variable in the final model for each carbon pool. For comparison, we also tested the effects of including the density of each of the two locally abundant non-threatened species—the desert fern legume (Fabaceae: *Lysiloma watsonii* Rose) and the Chihuahua oak (Fagaceae: *Quercus chihuahuensis* Trel.). This approach is recommended in general to detect species with an idiosyncratic effect on carbon storage (*i.e.,* effects not included via species contribution to CWM or functional divergence; cf. [14, 18]). Species were considered to have idiosyncratic effects on C storage if their inclusion significantly improved the predictive power (LOOCV and R^2) of the final regression model (after including other functional diversity measures such as CWM and FDiv [14]). In all statistical tests, we set significance level $\alpha = 0.05$. All analyses were run in R (R Foundation for Statistical Computing).

Results

The total ecosystem carbon (TEC) in our study system was considerable (70-130 Mg C ha^{-1}). The magnitude of carbon storage (above-ground biomass–AGC, soil–SOC, and TEC) decreased with elevation or slope steepness (Fig. 3a, Table 1). Aboveground-biomass carbon was negatively associated with functional divergence (FDiv), and SOC was positively associated with height (CWM.H) (Fig. 3b), causing TEC to be negatively related to FDiv and positively to CWM.H (Table 1a, b). The negative association of FDiv with carbon storage seems unexpected and is possibly due to the positive (but not significant) correlation of FDiv with an important predictor of AGC—elevation (Pearson's r = 0.24). The best models for SOC and TEC were not improved by adding the abundance of each of the threatened species. However, AGC was best explained by elevation with

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the inclusion of one of the evergreen (threatened) species abundance (*e.g.,* either the palm *Brahea aculeata* or the cycad *Dioon sonorense*) (Table 1c). In contrast, the two more common drought-deciduous species were not retained in any of the final carbon pool models.

Table 1. Final general linear models obtained for carbon pools based on environmental gradients and functional diversity. AGC = aboveground-biomass carbon, SOC = soil organic carbon, TEC= AGC + SOC, FDiv = multi-trait functional divergence index, CWM.H = community-weighted mean of height, LOOCV = prediction error using leave-one-out cross validation. *On a log scale.

Carbon pool models*	Model form	*P*	R^2_{adj}	LOOCV
a. Environment				
AGC =	3.57 – elevation (0.0006)	0.04	0.37	0.0196
SOC =	4.71 – slope (0.0104)	0.11	0.22	0.0680
TEC =	4.91 – slope (0.0089)	0.07	0.30	0.0377
b. Functional diversity				
AGC =	4.49 – FDiv (1.590)	0.06	0.32	0.0300
SOC =	3.35 + CWM.H (0.378)	0.05	0.36	0.1150
TEC =	5.48 – FDiv (1.914) + CWM.H (0.314)	0.04	0.52	0.0497
c. Environment + diversity				
AGC =	3.57 – elevation (0.0006)	0.04	0.37	0.0196
	3.48 – elevation (0.0007) + cycad (0.0072)	0.02	0.60	0.0235
	3.50 – elevation (0.0006) + palm (0.0060)	<0.01	0.73	0.0121
SOC =	3.71 – slope (0.0093) + CWM.H (0.3515)	0.02	0.60	0.0684
TEC =	4.34 – slope (0.0082) + CWM.H (0.2371)	0.03	0.56	0.0471

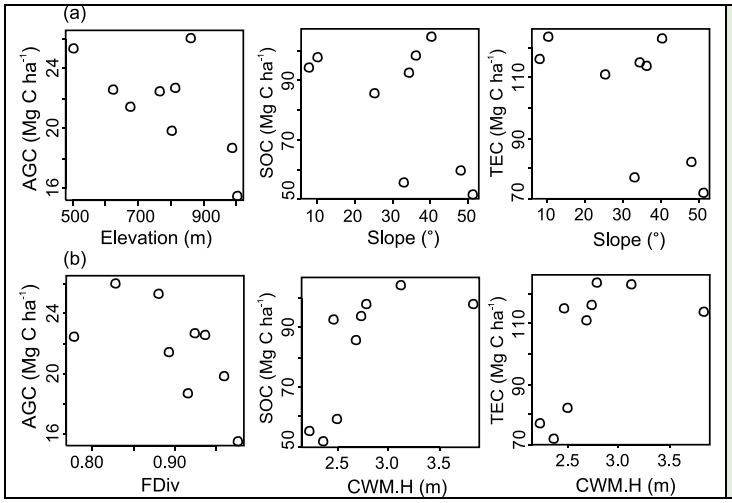


Fig. 3. Bivariate relationships of carbon storage pools with environmental gradients (a) and functional diversity components (b) that were retained as significant predictor variables in the final general linear models. AGC = aboveground-biomass carbon, SOC = soil organic carbon, TEC= AGC + SOC, FDiv = multi-trait functional divergence index, CWM.H = community-weighted mean of height.

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The two threatened plant species (cycad, palm) contributed considerably to the above-ground biomass carbon, 10-20% of total AGC per site (Fig. 4a). Therefore, predicting total AGC from non-threatened species alone would not account for a significant portion of above-ground biomass C (from threatened plant species), and it would not represent the overall pattern of AGC well, since the AGC of threatened and non-threatened species were not correlated (Pearson's r= 0.003, Fig. 4b).

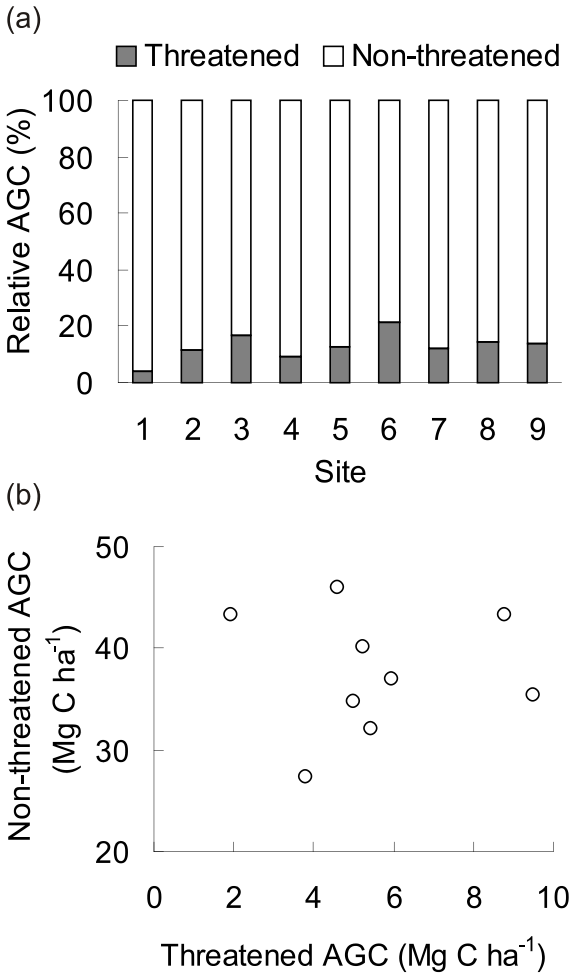


Fig. 4. Relative contribution of threatened and non-threatened plant species to total above-ground biomass carbon, AGC (a) and their bivariate relationship (b). Threatened plant species include the cycad *Dioon sonorense* and palm *Brahea aculeata* biomass, non-threatened plant species includes 54 common plant species. See methods for additional details.

Discussion

In agreement with our findings, above-ground biomass and productivity in tropical forests have been shown to decrease along gradients of elevation and slope steepness, most likely through microclimatic and soil nutrient constraints on plant physiology [19, 20]. At broader (sub-continental) geographical scales, tropical dry forests have been characterized by the positive association of live above-ground biomass with mean annual precipitation [21]. In contrast to the effects of environmental gradients, the effects of functional diversity (or its various components) on carbon storage and ecosystem function have been studied less in field settings in tropical ecosystems and yielded no consistent patterns [14, 22]. One of the few emerging generalizations from this and other recent studies appears to be that stem traits such as CWM of height or

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diameter can better predict above-ground biomass and other carbon pools compared to CWM of leaf traits (*e.g.*, leaf N) or even to multi-trait functional diversity indices such as FDiv [22, 23].

Although every plant, be it common or rare, has the capacity to contribute to overall carbon storage, our results offer evidence that two highly threatened plant species (*i.e.*, cycad, palm) can contribute considerably to the above-ground biomass carbon despite their endangered status, because they can be locally abundant. Furthermore, several lines of evidence suggest that the long-term loss of carbon storage capacity due to the removal of threatened species (*e.g.,* by ongoing harvesting of cycad seedlings for illegal trade in ornamental plants) may not be easily offset by non-threatened species. First, the abundance of two common drought-deciduous species (*L. watsonii* and *Q. chihuahuensis*) was not retained in any of the final carbon pools models. Second, adding the abundance of cycad and palm species significantly improved the predictability of carbon storage because it accounted for variance unexplained by functional divergence (FDiv), height (CWM.H), or elevation, variables more frequently used in studies modeling carbon storage [14, 22, 23]. Third, contrary to the exploitative strategy of the more dominant drought-deciduous species, the evergreen habit and long life-span of both the cycad *Dioon sonorense* and the palm *Brahea aculeata* suggest that they may contribute to the regional carbon cycle through longer-term carbon storage and slow C release [23]. Finally, in addition to carbon storage, long-lived threatened species such as cycads and palms can contribute to other ecosystem functions and services such as (*i*) soil retention and water filtration [24], (*ii*) maintenance of functional (trait) and genetic diversity [4], and (*iii*) amelioration of heat stress and facilitation of tree seedling establishment [8]. Thus, our data lend additional support to the idea that species identity matters to the functioning and productivity of seasonally dry tropical forests.

Our conservative TEC pools estimates (TEC = 70 – 130 Mg C ha^{-1}) varied widely with topography, and our highest estimate was close to the values reported for more mesic old-growth SDTFs in Chamela (TEC = 141 Mg C ha^{-1} [25]) and Yucatan (TEC = 153 Mg C ha^{-1} [26]) in Mexico. On the other hand, our estimated TEC values tended to be above the values reported for primary forests in the semiarid Argentinian Chaco (TEC = 60 – 85 Mg C ha^{-1} [14]). In all the above cases, SOC contributed at least 50% C to the TEC pool, and this percentage was even higher for the drier sites (*i.e.*, our studied and the Chaco forests). Because our models were developed for understanding the system, not for scaling up biomass estimations, generalizations should be taken with care. However, although R^2 values may not always be the best indicators of model performance or fit, our models with the highest R^2 consistently had both the lowest p value and lowest prediction error, especially for models that included the abundance of threatened species. Therefore, our findings suggest that the effects of endangered species may be as important in affecting local carbon pools as other studies have found for some non-threatened species with idiosyncratic effects on ecosystem functioning in SDTFs [14]. Consequently, a decline in the abundance of threatened species with long life-spans (*e.g.,* cycads, palms) could dramatically influence local biodiversity and negatively affect ecosystem function and provision of other ecosystem services beyond carbon storage (*e.g.*, improved water quality, soil protection, or ecotourism).

Implications for conservation

Threatened species are usually the main target of conservation science, with a species-centered approach combining demography, genetics and habitat evaluation. Our study suggests that the functional role of threatened species should be investigated and possibly incorporated into conservation management plans at the species and ecosystem levels. We therefore recommend

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more research on globally and regionally rare and threatened plant species that can become locally abundant and contribute significantly to ecosystem functions (*e.g.*, carbon storage). Long-term maintenance of biodiversity (sensu lato) can play a significant role in ecosystem functioning and human well-being, especially in closely coupled natural-human systems such as Biosphere Reserves. Synergies should be sought between international conservation initiatives with parallel or overlapping objectives in biodiversity conservation and ecosystem functioning (*e.g.*, the United Nations MAB and REDD+ programs) to maximize resources while meeting multiple conservation goals.

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