Trade-offs between savanna woody plant diversity and carbon storage in the Brazilian Cerrado

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Abstract

Incentivizing carbon storage can be a win-win pathway to conserving biodiversity and mitigating climate change. In savannas, however, the situation is more complex. Promoting carbon storage through woody encroachment may reduce plant diversity of savanna endemics, even as the diversity of encroaching forest species increases. This trade-off has important implications for the management of biodiversity and carbon in savanna habitats, but has rarely been evaluated empirically. We quantified the nature of carbon-diversity relationships in the Brazilian Cerrado by analyzing how woody plant species richness changed with carbon storage in 206 sites across the 2.2 million km^2 region at two spatial scales. We show that total woody plant species diversity increases with carbon storage, as expected, but that the richness of endemic savanna woody plant species declines with carbon storage both at the local scale, as woody biomass accumulates within plots, and at the landscape scale, as forest replaces savanna. The sharpest trade-offs between carbon storage and savanna diversity occurred at the early stages of carbon accumulation at the local scale but the final stages of forest encroachment at the landscape scale. Furthermore, the loss of savanna species quickens in the final stages of forest encroachment, and beyond a point, savanna species losses outpace forest species gains with increasing carbon accumulation. Our results suggest that although woody encroachment in savanna ecosystems may provide substantial carbon benefits, it comes at the rapidly accruing cost of woody plant species adapted to the open savanna environment. Moreover, the dependence of carbon-diversity trade-offs on the amount of savanna area remaining requires land managers to carefully consider local conditions. Widespread woody encroachment in both Australian and African savannas and grasslands may present similar threats to biodiversity.

Keywords: biodiversity, carbon-biodiversity cobenefits, carbon sequestration, cerrado, forest, savanna, woody encroachment

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Introduction

Savannas are responsible for globally significant carbon fluxes, and the balance between carbon sequestration via plant biomass accumulation and emission via biomass burning influences the trajectory of the global land carbon sink (Van Der Werf *et al.*, 2010; Liu *et al.*, 2015). The great capacity for carbon storage in savannas (Scurlock & Hall, 1998) as well as the perception of savannas as degraded landscapes (Sasaki & Putz, 2009) has raised the issue of their possible management for carbon sequestration (Midgley & Bond, 2015; Veldman *et al.*, 2015a,b).

In some ecosystems (e.g., tropical forests), promoting carbon storage may lead to greater biodiversity, thus bringing conservation-climate mitigation cobenefits (Venter *et al.*, 2009; Gilroy *et al.*, 2014). In the savanna ecosystem, which is defined as having sparse tree cover and a continuous herbaceous layer (Scholes & Archer, 1997; Bond, 2008), the relationship between diversity and carbon is more complex. Across savannas globally,

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fire suppression generally leads to woody thickening and eventually forest encroachment in areas with sufficient rainfall (Higgins *et al.*, 2007; Bradstock & Williams, 2009; Staver *et al.*, 2011); during this process, there is substantial carbon accumulation in above- and belowground pools (Grace *et al.*, 2006; Heckbert *et al.*, 2012; Pellegrini *et al.*, 2014) and a rapid colonization by tree species typical of forests (Moreira, 2000; Rodrigues-Souza *et al.*, 2015). However, the plant species adapted to the open savanna habitat tend to be excluded from the ecosystem during forest formation (Durigan & Ratter, 2006; Hoffmann *et al.*, 2012; Rodrigues-Souza *et al.*, 2015).

Management strategies that promote carbon sequestration could have significant consequences for savanna plant species in the Brazilian Cerrado—a biodiversity hotspot spanning >2 million km^2 with specially adapted plant and animal communities, many of which are found nowhere else on Earth (Myers *et al.*, 2000; Ratter *et al.*, 2006). Loss of plant species from the Cerrado region due to land-use change has previously been reported (Klink & Machado, 2005), but recent fire suppression and subsequent forest encroachment are

increasingly pressing threats (Durigan & Ratter, 2006, 2015; Pinheiro & Monteiro, 2010). Governmental fire prevention measures, with encouragement from non-governmental organizations (Veldman *et al.*, 2015b), risk triggering widespread declines of plant species that are adapted to the open savanna habitat and thus dependent on disturbance by fire (Parr *et al.*, 2014; Durigan & Ratter, 2016; Veldman *et al.*, 2015a,b). At the same time, fire in the Cerrado region contributes substantially to annual greenhouse gas emissions (Van Der Werf *et al.*, 2010), and carbon sequestration from fire suppression may constitute a large sink offsetting emissions (Grace *et al.*, 2006; Pellegrini *et al.*, 2014). The simultaneous loss of savanna species, gain in forest species, and gain in ecosystem carbon stocks resulting from woody thickening and forest encroachment during fire suppression produces a conservation dilemma.

The decision to manage the Cerrado and numerous other savanna landscapes globally (see Veldman *et al.*, 2015b) for either carbon or endemic savanna species diversity has large implications for both climate change and the preservation of thousands of plant species; however, the severity and nature of the trade-off between savanna endemic diversity and carbon remain unknown. Quantitative evaluation of this trade-off is critical because (i) the magnitude of savanna endemic diversity losses will determine the absolute diversity cost of gaining carbon and (ii) the nature of the relationship between carbon and savanna species biodiversity will determine the stage of carbon accumulation (e.g., initial vs. final) where losses are most severe.

To address the issue, we quantified how the diversity of woody plants change with increasing carbon storage using a dataset of >18 000 observations of 1797 species censused at 206 sites (totaling 209 ha in area sampled) distributed across savannas and forests spanning the 2.2 million km^2 Cerrado region (Fig. S1). We utilize a space-for-time substitution by sampling plots spanning a range of woody plant biomass (open savanna to dense forest) under the assumption that in terms of their carbon storage and species composition, the plots mimic the outcome of different approaches to fire management on plots of Cerrado that are currently savanna (e.g., Moreira, 2000; Henriques & Hay, 2002; Pellegrini *et al.*, 2014). We consider changes in diversity and evenness of woody plant species adapted to savannas or forests (i.e. savanna species diversity vs. forest species diversity) as well as total species diversity (i.e., all woody plant species) using multiple diversity indices. We hypothesize that (i) increases in total species diversity with carbon gains will mask large losses of species endemic to savannas and (ii) the rate of change in diversity will depend on the standing amount of woody biomass and the remaining area of savanna.

To test our hypotheses, we analyzed the impact of carbon accumulation on different components of diversity at two spatial scales. At the local scale, we measured how the richness of the woody plant species adapted to savanna or forests (i.e., savanna or forest guild) or total woody plant diversity changes with increasing carbon stocks at the plot level (i.e., due to woody thickening). At the regional scale, we measured how the richness of woody plant species in savanna and forest landscapes changed with increasing carbon due to converting savanna area into forest (i.e., due to woody or forest encroachment).

Materials and methods

Quantifying biodiversity

The Cerrado region in Brazil (Fig. S1) spans a large climatic gradient (ranging from semi-arid to mesic environments), with the core region receiving ~1400–1600 mm mean annual precipitation and a pronounced dry season from May to September (Oliveira & Marquis, 2002). The Cerrado region contains a number of vegetation formations that differ in structure and species compositions, the most prominent being savannas and forests, which we here refer to as biomes. Although the herbaceous layer contains a wealth of species (Durigan & Ratter, 2016), we focus on woody plants (shrubs and trees, generally >5 cm in basal diameter) in savannas and forests because they are critical carbon storage reservoirs for the land carbon sink (Dixon *et al.*, 1994) and one of the essential criteria for defining the Cerrado region as a biodiversity hotspot (Myers *et al.*, 2000).

In order to analyze how woody plant diversity changes with woody biomass, we compiled and analyzed a plant biodiversity database containing complete floristic surveys from savanna, woodland (referred to as cerradão in Brazil, which contains intermediate tree cover and biomass between savanna and forest), and forests from 206 sites with minimal anthropogenic disturbance (e.g. located in protected areas or in sites where the authors did not note cultivation and/or deforestation). These plots were distributed across the Cerrado region and into the adjacent Atlantic Forest region with similar environments (Fig. S1; references listed in Table S1). Forests spanned a range of types including riparian, semi-deciduous, and dry forests (montane and rainforests were excluded). These plots span a woody biomass gradient from open savanna to dense forest.

Plant species in forests tend to be shade-tolerant but fire-sensitive, while savanna species are relatively fire-tolerant but shade-intolerant (Hoffmann *et al.*, 2012). As a result of these differences, distinct plant communities occupy forest and savanna biomes, with few generalist species capable of thriving in both (Hoffmann *et al.*, 2012). Due to the potential biases and inconsistencies in the 'expert opinion' approach to classification, we classified species as belonging to savanna or forest functional guilds based on their relative occurrences in savanna or forest vegetation formations using a species

association index (Cáceres & Legendre, 2009). The association index statistically evaluates whether species occur in a particular habitat disproportionately more than would be expected by chance. The species classifications were then used to quantify plant species in each site as savanna species or forest species.

We were unable to classify species that were generally rare in either savanna or forest plots due to a lack of statistical power (e.g., ~70% of the unclassified species occurred less than three times). For the more abundant unclassified species, we assessed the potential of incorporating them into guilds based on a plant diversity database (Flora do Brasil, 2015). We discuss this potential classification procedure in detail in the Supplementary Information; but briefly, of the unclassified species that occurred >5 times, ~40% of the species were classified as occurring in a 'dense' vegetation in Flora do Brasil, which can be interpreted as a dense savanna woodland, an ambiguous definition to be included in an analysis of species preferences. Due to the variety of different environmental conditions that this classification may be referring to, we maintain the conservative assumption that the unclassified species cannot robustly be categorized into either savanna or forest guilds.

Importantly, although the number of unclassified species limits our ability to quantify exact changes in species richness, there were substantially fewer unclassified species than classified species in both savanna plots (20% unclassified vs. 53% classified as savanna-guild species) and forest plots (21% unclassified vs. 68% as forest guild species).

Quantifying carbon in aboveground woody biomass

For each site in the database, we quantified aboveground carbon in woody biomass using allometric relationships. We employed a general allometric equation for tropical savannas that has been used to calculate woody biomass stocks in savannas (Supplementary Information; Lehmann *et al.*, 2014). Although savanna and forest species can differ in their foliar biomass allometries (i.e., leaf biomass per-unit stem diameter), we know of no evidence that they differ in woody biomass. As such, we used the same allometric equation for forest species for consistency. This equation also expresses woody biomass as a function of total basal area in a plot, thereby allowing us to quantify biomass in studies that do not present stem diameter measurements of individuals.

Here, we focus on woody biomass as the primary changing carbon pool for two reasons. First, shifts in carbon storage in the woody biomass pool occur on timescales most relevant for mitigating carbon emissions (Pan *et al.*, 2011). Second, other vegetation carbon pools such as the herbaceous layer are small in comparison to changes in woody biomass carbon (e.g., woody biomass can increase from 10 to 100 MgC ha^{-1} while herbaceous biomass losses only amount to ~3 MgC ha^{-1}; Pellegrini *et al.*, 2014). Finally, soil pools can increase with forest development (a previous study found gains of ~30 MgC ha^{-1} across a gradient in forest growth [Pellegrini *et al.*, 2014]), but the generality of these changes needs to be verified before incorporated into a full analysis (Silva *et al.*, 2013). We discuss the implications below.

Calculating species richness at the local scale

To quantify woody plant species richness at the local (plot) scale, we first standardized measures of local species richness to a common area of 0.5 ha because the inventories at each plot varied in the total area surveyed (median of 1 ha; interquartile range 0.7–1.2). A spatial scale of 0.5 ha was chosen because (i) smaller plots tend to inaccurately capture both true species diversity and carbon storage (Wagner *et al.*, 2010) and (ii) a large number of the plots compiled from the literature exceed this size threshold (n = 169 of 206). To calculate standardized measures of species richness at the 0.5 ha plot scale, we removed plots smaller than 0.5 ha, resulting in 169 plots with a median area of 1 ha. For all plots larger than 0.5 ha, we rarefied individuals out of the plots to create a set of resampled half-hectare plots. In order to calculate stem densities in plots rarefied to 0.5 ha, we determined the number of stems expected within a half-hectare for each plot by rescaling the original density of stems within each plot to a half-hectare, removing individuals at random until the density was achieved.

Because we were interested in quantifying species richness of both the savanna and forest guilds as well as total species richness (i.e., all woody plants in a plot), we performed this analysis three times in separate rarefactions to determine the species richness of (i) savanna guild species, (ii) forest guild species, and (iii) all woody plant species. To explore whether other indicators of biodiversity and community composition change with carbon, we also calculated Shannon's diversity index and Pielou's evenness index.

We used maximum likelihood methods to model the relationship between carbon storage and the richness of the savanna guild, forest guild, and total species at the plot scale. Because we were concerned with accurately capturing the precise shape of the relationship between carbon and species richness, we analyzed multiple models with different functional forms to compare both linear and nonlinear changes. We used five functional forms that are observed during species turnover through succession: saturating, linear, quadratic, logarithmic, and sigmoidal (see Supplementary Information for exact functional forms). We used the Akaike information criterion (AIC) to compare the performance of these five models. All analyses were performed in R using the *anneal* function in the *likelihood* package (R Development Core Team, 2010).

To evaluate possible spatial autocorrelation of the model fits, we calculated the Moran's I on model residuals. Following a significant signature of spatial autocorrelation, we inspected a correlogram to determine the minimum necessary separation between sites to eliminate spatial autocorrelations (Hua *et al.*, 2015). We then used this minimum distance to resample groups of plots sufficiently far apart, which we then fit with the appropriate selected model (see Supplementary Information for a full explanation). We iterated this process 100 times to generate means and confidence intervals on the fitted parameters and goodness of fits on the full model and compared the resampled model to the full dataset model to evaluate whether our conclusions were robust to autocorrelation.

Calculating species richness at the landscape scale

To quantify how species richness changed with increasing carbon storage at the landscape scale, we assumed the landscape area could be broadly defined as either savanna or forest (Staver *et al.*, 2011). We do not explicitly account for the intermediate formation of woodland vegetation, which is relatively limited in extent compared to the distribution of savanna and forest (Hirota *et al.*, 2010, 2011). To quantify the number of species in savanna, we generated an individual-based species accumulation curve for savanna tree species across all plots within the savanna biome, excluding species classified as forest guild species. We then repeated these analyses by quantifying the number of species in forest in a similar fashion, excluding species classified as belonging to the savanna guild (Supplementary Information; Fig. S2).

In contrast to our local-scale species richness analyses, here we included unclassified species present in either the savanna or forest plots in analyses of landscape-scale richness because these unclassified rare species can make large contributions to landscape-scale biodiversity (Bridgewater *et al.*, 2004). Overall, the unclassified species represent 47% of total species found in savanna and 52% of total species found in forest. Importantly, 75% of the unclassified species only occurred in either savannas or forests (i.e., not in both), thereby minimizing double counting of species that may occur in both forest and savanna.

To quantify the number of species throughout the landscape, savanna and forest species accumulation curves were fit with a power-law function, as predicted from theoretical expectations of species-area curves (Tjørve, 2009 and see Supplementary Information), using a nonlinear least-squares model to estimate parameters. These species accumulation curves were then used to extrapolate the number of species in a landscape based on the expected number of individuals in the landscape, determined by multiplying an average density of individuals (calculated for savanna and forest from the empirical data) by the total area of either savanna or forest. As a robustness check to this extrapolation approach, we performed a swapping rarefaction of the actual plots (see Supplementary Information for a detailed description) to verify the nonlinearity while preserving local abundance distributions and allowing that savanna species might persist in forests.

To obtain estimates of species richness at the landscape scale relevant to the current conservation efforts in the Cerrado region, we examined the IUCN-designated protected areas (PA; categories I and II, $n = 74$) in the Cerrado region. Within each PA, we determined the area of savanna and forest (using 50% tree cover as a break point, *sensu* Hansen *et al.*, 2013) using a high-resolution (~30 × 30 m) LANDSAT satellite product of tree cover (Hansen *et al.*, 2013). We then determined species richness in savanna and forest in each PA using the method described above. These estimates were used to quantify the potential trade-offs between savanna species richness and carbon accumulation and explore the variability across PAs.

Results

At the local scale, the total number of woody plant species increased with plot biomass. The best fit curve was a quadratic function ($r^2 = 0.32$), illustrating that initial gains in total richness were rapid but began to saturate at high biomass values (Fig. 1a). It is unlikely that the slight decline in the fitted quadratic at high biomass values is biologically meaningful given the high diversity of mature forests in this region (Ratter *et al.*, 2006). A logarithmic function with saturating total richness at high biomass values explained similar levels of variance ($r^2 = 0.30$) but was not chosen because it had a higher AIC (Table S2).

The increase in overall plot biodiversity concealed large losses in the savanna guild. Species richness of the savanna guild declined monotonically and nonlinearly as carbon stocks increased ($r^2 = 0.36$, Figs 1b and S3). Initially, the decline in savanna species richness with increasing carbon storage was rapid, but decelerated as carbon stocks continued to increase and species became rarer (Fig. 1b, c). In contrast, the richness of the forest guild increased rapidly with carbon storage at low carbon density, but saturated with increasing carbon ($r^2 = 0.44$, Figs 1b, c and S3).

Analyses of the Shannon diversity index produced similar patterns: a nonlinear trade-off between gains in total species diversity and losses of savanna-guild diversity (Supplementary Information, Fig. S4). Evenness did not significantly change across the gradient for the total woody plant community, species in the savanna guild, or species in the forest guild (Supplementary Information, Fig. S5). Given the consistencies between the Shannon diversity index and total richness, we focus on total richness for further analysis.

We next evaluated whether spatial autocorrelation may be influencing the richness-carbon relationship. Moran's I indicated significant autocorrelation in the residuals of the model between species richness and carbon (Supplementary Information). Inspection of the autocorrelation using a correlogram illustrated that a minimum distance of 300 km between plots was required for residuals to be independent. Repeated random resampling of independent plots (i.e., plots separated by >300 km) and fitting with maximum likelihood indicated that spatial autocorrelation did not substantially affect fits for the forest guild, savanna guild, and total species richness (Fig. S6; Table S4); the full dataset model fell within the confidence intervals of the resampled model ensemble (Fig. S6) and differences in the fitted coefficient values were minor (Tables S3 and S4). Moreover, the mean goodness of fit (r^2) values of the resampled models were similar to those obtained from the full dataset model (Table S4). Consequently, the resampled models were consistent with the full model and we conclude our model results are robust to possible spatial autocorrelation.
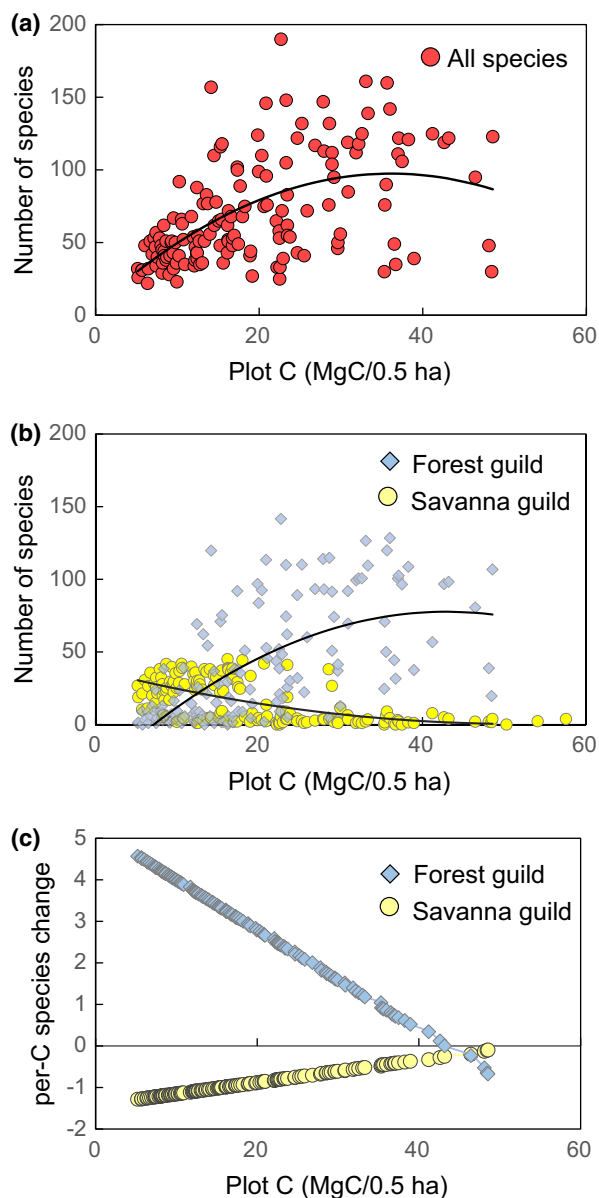
Fig. 1 (a) Species richness of total woody plant community with fitted quadratic ($r^2 = 0.32$, $n = 151$); (b) changes in species richness for savanna and forest guilds as a function of plot carbon with fitted quadratics (savanna: $r^2 = 0.36$, $n = 151$; forest: $r^2 = 0.44$, $n = 151$). Richness was determined by subsampling plots down to a common plot size of 0.5 ha (Supplementary Information). Curves fitted using maximum likelihood with model selection. (c) local-scale carbon-diversity trade-offs using model estimates of the change in number of savanna and forest guild species relative to change in carbon. Dots represent each predicted value from a plot, colored by species guild.

We next considered how diversity of species in a savanna landscape may change if savanna area was lost due to forest encroachment. From the rarefaction analysis, we found that savanna species richness rose

rapidly with increases in the abundance of individuals but that the rates of accumulation declined with increasing abundance of individuals (Fig. 2a). Correspondingly, there was an exponential decline in savanna species richness losses per unit carbon gain and increasing total savanna area within a PA (Fig. 2b). Small PAs (e.g., <100 hectares) showed dramatic losses of savanna species with carbon gains (Fig. 2b), illustrating the sensitivity of particular PAs to carbon gains. On the other hand, large PAs displayed much less pronounced reductions in savanna species richness with increasing carbon, resulting in substantial variability in the sensitivity of savanna species richness to a fixed absolute amount of forest encroachment across PAs (Figs 2c and S7). We confirmed the nonlinear nature of these declines in savanna species richness using an additional approach that accounted for the potential for savanna species to exist in forest plots (Supplementary Information).

The loss in savanna species richness was mirrored by strong gains in forest species richness with increasing forest area. Importantly, however, the ratio of forest species gains vs. savanna species losses was dependent on the total size of the area being considered. When the combined area of savanna and forest was small, gains in forest species richness with increasing forest area were greater than the losses of savanna species richness (Fig. 3a). In contrast, when the combined area of savanna and forest was large, gains in forest species richness with increasing forest area were less than losses of savanna species richness (Fig. 3b). Consequently, in locations with relatively small areas of forest and savanna, the number of forest species gained exceeds the number of savanna species lost per unit of carbon gained; however, in locations with large areas of both savanna and forest, the number of savanna species lost exceeds the number of forest species gained per unit of carbon gained.

To illustrate the variety in the potential ratio of forest species gained vs. savanna species loss per unit of carbon gained, we determined the ratio across the PAs, which vary in size and proportional areas of savanna and forest (Fig. 3c). Our ability to quantify the ratio in each PA is limited by the extrapolation that we can make with our species accumulation curves, but, once again, the qualitative nature of these functional forms will produce this trade-off function. For the PAs that contained estimated individuals within the bounds of our species accumulation curves (Fig. S2), the calculated ratios ranged from 0.2 to 8.1 (Fig. 3c), with values <1 indicating reserves where savanna species losses exceeded forest species gains with increasing carbon (calculated to be 39 PAs, Fig. 3c).
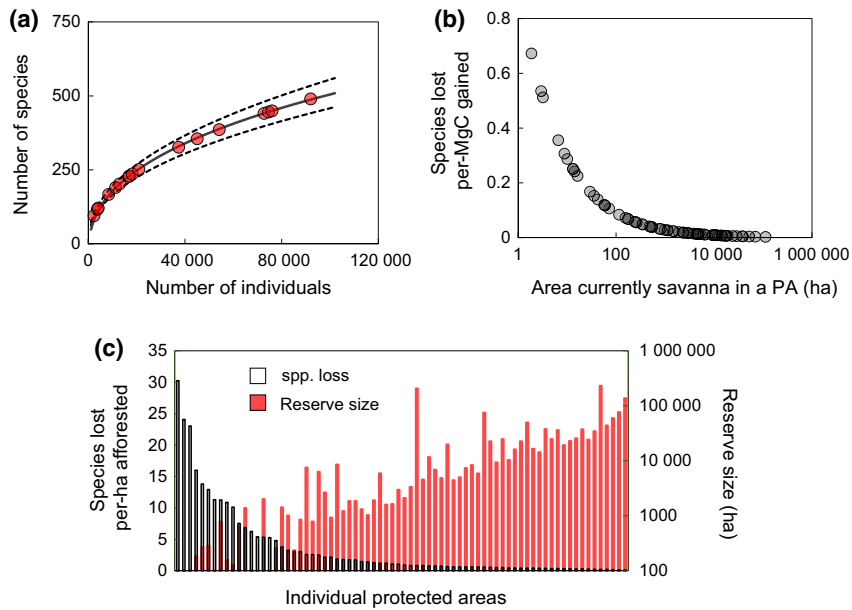
Fig. 2 (a) Sample-based rarefaction of total species richness in savanna sites, expressed as a function of individuals. Red dots indicate the estimated richness of Cerrado protected areas given total savanna area and corresponding estimated abundance of individuals in each PA ($n = 72$, Supplementary Information). (b) Relationship between the number of species lost per-MgC gained within a landscape as a function of total savanna area within Cerrado PAs. (c) Comparison of the distribution of species lost per-ha converted from savanna to forest (gray) with park area (red) across the Cerrado PAs. The loss rate is a function of the total savanna area within a PA. The total size of the PA sets a limit on the potential losses, but within PAs of equivalent sizes there can be large variability due to the actual amount of savanna area (in this case relative to forest area).

Discussion

Taken together, these results illustrate that managing for carbon and biodiversity in tropical savannas produces an important conservation dilemma. Overall, and as expected, there is a general trend for total woody plant biodiversity to increase with carbon storage. The gains in total diversity were driven by increases of woody plant species adapted to forests, which were substantial enough in magnitude to overcompensate for the losses of woody plant species adapted to savannas. The loss of plant species that exclusively occur in the open savanna biome presents a key carbon-biodiversity trade-off. While savanna-guild species always decline during afforestation by definition, our results reveal important nonlinearities in how savanna species decline with increasing carbon accumulation.

Rates of savanna species losses at the plot scale are steepest during the initial stages of woody thickening, while rates of savanna species losses at the landscape scale are steepest at the final stages of forest encroachment (Figs 1b, c and 2b). Accordingly, where carbon sequestration is a priority, it is best implemented by maximizing sequestration at the plot scale in localized areas while minimizing the total area encroached.

At the landscape scale, the saturating relationship between forest species diversity and carbon results in diminishing returns of carbon gains and forest species gains as the amount of forested area increases. On the other hand, declines in savanna species richness only continue to accelerate. As a result, the number of forest species gained becomes equal to the number of savanna species lost. This represents an important transition point, past which managing for carbon will likely result in larger savanna species losses than gains in forest species per unit of carbon stored.

The transition point thus signifies a threshold separating contrasting outcomes of (i) maximizing carbon while realizing modest forest diversity gains and considerably greater losses of savanna species, or (ii) restricting forest regrowth and carbon storage potential while retaining a large amount of savanna species diversity. Land managers seeking to balance the multiple objectives of carbon storage and maintenance of savanna species diversity should prioritize this second outcome, managing the landscape in reserves below this threshold. Although our sample size limits our ability to provide an exact quantitative assessment of each PA, as long as the exponent of the fitted species accumulation curve in savannas exceeds that of forests, this threshold will occur. In turn, quantifying this tran-
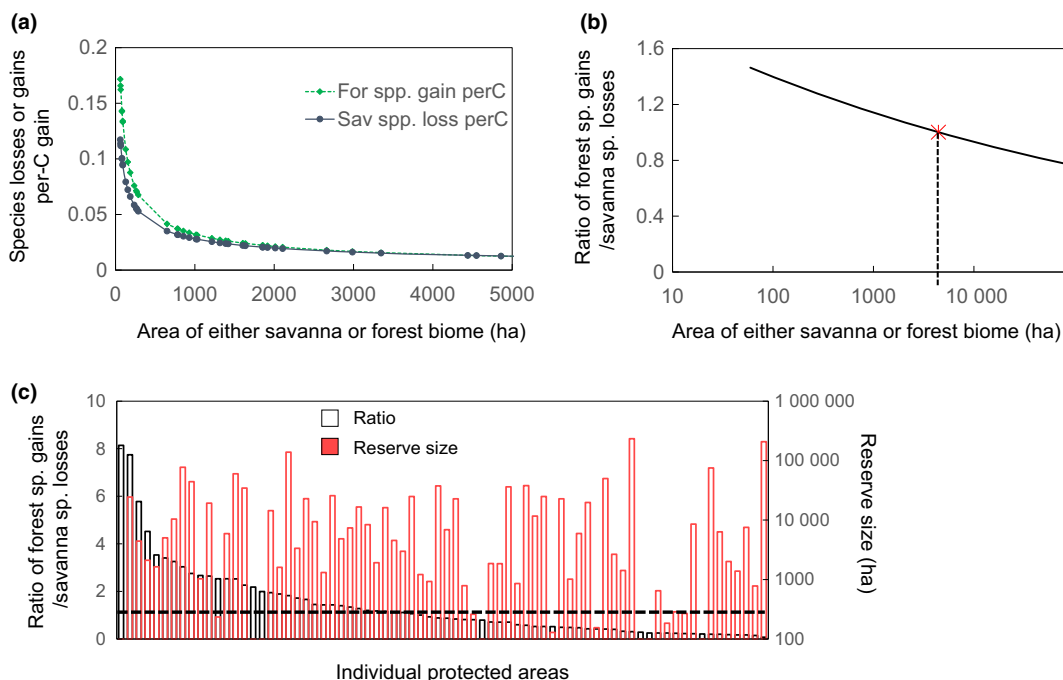
Fig. 3 (a) Gains vs. losses of species richness per-unit carbon gain for savanna and forest species at the landscape scale. Forest species richness increases per-C gain, and is expressed as a function of forest biome area; savanna species richness decreases per-C gain, and is expressed as a function of savanna biome area. (b) Ratio of per-carbon richness changes of forest vs. savanna species [the ratio of the two curves in (a)] as a function of existing biome area. Red asterisk illustrates intersection at ~4440 ha. (c) Distribution of ratios (species richness changes of forest vs. savanna species per-unit C gain) across the protected areas (black bars, primary axis) with the corresponding size of the PA (red bars, secondary axis, $n = 72$). Dashed line indicates a ratio of one.

sition point based on surveys within specific reserves undergoing forest encroachment (e.g., Durigan & Ratter, 2006) would be a useful next step to identify the relative biodiversity costs and benefits by promoting carbon storage.

Studies documenting composition shifts during woody thickening and biomass accumulation have found inconsistent and sometimes contrasting changes in the woody plant diversity of the savanna guild, including increases, no change, or decreases (Moreira, 2000; Roitman *et al.*, 2008; Rodrigues-Souza *et al.*, 2015). Disagreement among studies may be due to a number of factors, such as the initial woody plant biomass in a plot (and thus how quickly the canopy closes and savanna species become excluded) and the length of the study period (sufficient enough time to allow for substantial shifts in vegetation structure and subsequent turnover in community composition; Durigan & Ratter, 2006). Here, using a space-for-time substitution, we find that the richness of woody plant species endemic to the savanna biome does not benefit from woody thickening and on average savanna species richness declines quickly across plots increasing in woody biomass. The replacement of savanna species by forest species during carbon accumulation

in a plot reflects the effective competitive exclusion of the slow-growing shade-intolerant savanna species by fast-growing shade-tolerant forest species. This is likely reflective of the faster growth and colonization ability of forest species, whose recruitment can greatly outpace savanna species (Roitman *et al.*, 2008; Hoffmann *et al.*, 2012).

Quantitative predictions of carbon-diversity relationships at the landscape scale might be made more accurate by accounting for spatially structured tree beta diversity within the Cerrado (Ratter *et al.*, 2003; Bridgewater *et al.*, 2004). Beta diversity in savannas in the Cerrado is estimated to be high, with previous studies finding 35% of recorded species to occur in a single site only (Ratter *et al.*, 2003), and Sørensen similarity indices to range from 0.37 to 0.625 in the core Cerrado region (Bridgewater *et al.*, 2004), illustrating high species turnover. While we do not calculate beta diversity here, given the potential limitations arising from extrapolating across space in areas where plots are infrequent (Fig. S1), we found a similar pattern of rare species contributing a large amount to overall richness. Because our sites spanned the entire Cerrado region, the overall species accumulation curve from which our estimates were drawn may be steeper than the species accumula-

tion curve within each PA (owing to higher spatial turnover of species across the Cerrado than within a local PA; Bridgewater *et al.*, 2004; Ratter *et al.*, 2003). Nevertheless, the main finding of nonlinear declines in savanna-guild richness with carbon accumulation is unlikely to change.

The large variability in the sensitivity of savanna-guild diversity to carbon accumulation across PAs points to the need to consider heterogeneity in potential carbon-diversity relationships across PAs (Fig. S7). Spatially explicit analyses of species diversity in the Cerrado savannas have found evidence for certain areas being especially rich in woody plant diversity (Ratter *et al.*, 2010). Moreover, potential carbon storage in forests also varies across the Cerrado (Pellegrini *et al.*, 2016). Combining maps of species richness with potential carbon storage would be one useful step to identifying areas where the trade-offs are likely to be most severe. Spatial analyses will also improve the evaluation of potential species losses in individual PAs.

Comprehensive conservation planning in the Cerrado must also take into account other plant guilds such as the highly diverse herbaceous species, as well as animal groups. The savannas of the Cerrado are exceptionally diverse in herbaceous species (Ratter *et al.*, 1997), which tend to be highly light sensitive and thereby likely to be excluded during woody thickening and forest encroachment. Recent work has identified the afforestation of grasslands as a critical conservation issue, with losses of herbaceous species being one unequivocally negative consequence (Durigan & Ratter, 2016; Veldman *et al.*, 2015b). Globally, grasslands have diverse herbaceous layers (Veldman *et al.*, 2015b) and consideration of declines in herbaceous species richness will be critical. Future studies should attempt to capture the complete biodiversity consequences of woody thickening, which is likely to strengthen the relationship between carbon accumulation and savanna endemic declines and possibly negate the net-diversity gains in total plant species with increasing plot carbon altogether.

Consideration of carbon pools in nonwoody vegetation will also help further refine the carbon-diversity relationship. Carbon stored in soil layers can be substantial in grassy ecosystems (Jackson *et al.*, 2002; Pellegrini *et al.*, 2015), with the majority of total ecosystem carbon in the savanna existing in belowground pools (Grace *et al.*, 2006). However, carbon in plant pools tend to be the most responsive to changes in disturbance regime (Higgins *et al.*, 2007) and shift on timescales relevant for mitigating carbon emissions (Pan *et al.*, 2011). These gains in carbon can offset the loss in the herbaceous layer ($\sim$2–3 MgC ha^{-1}). Furthermore, forests in general tend to have higher soil carbon than

savannas in the Cerrado region, which accumulates during woody biomass accumulation and forest encroachment. For example, a previous study estimated gains of $\sim$30 MgC ha^{-1} in the upper soil from open savanna to closed-canopy transitional forest (Pellegrini *et al.*, 2014). Subsequently, while we might expect gains in soil carbon to follow gains in woody biomass carbon, the loss of belowground herbaceous biomass in deeper soil layers can sometimes offset ecosystem carbon gains (Jackson *et al.*, 2002), requiring large-scale measurement before generalities can be made.

The potential impact of fire on offsetting the carbon gains during woody thickening and forest encroachment needs to be considered as well. Woody plant species adapted to savannas can accumulate thick bark and grow quickly enough to survive fire (Hoffmann *et al.*, 2009) forming relatively fire-resistant stable carbon pools. In contrast, forest trees invest less biomass in bark, and consequently are more sensitive to dying during a fire event because their bark thickness is insufficient to protect their cambium from overheating (Brando *et al.*, 2012; Pellegrini *et al.*, 2016). As a consequence, the increase in carbon during woody thickening will be at high risk of being lost due to burning, even once forests have formed. Forest fires in this region occur regularly and are expected to increase with shifting climates and greater droughts (Alencar *et al.*, 2011, 2015). When forests do burn, large amounts of carbon can be lost (Kauffman *et al.*, 1993; Morton *et al.*, 2013) and thus the expected gains in carbon may be greatly diminished over the long term (Pellegrini *et al.*, 2016). This may result in significant reductions in the effective number of forest species gained per unit carbon stored over the long term.

Our space-for-time substitution allowed for the comparison of a large number of plots across a large spatial scale, a method employed in other carbon-diversity studies (e.g., Gilroy *et al.*, 2014). This is specifically a space-for-time substitution under the scenario of fire exclusion and woody encroachment, which is a reasonable expectation given current management (Durigan & Ratter, 2006, 2016) and the trajectory of biomass accumulation during exclusion (Moreira, 2000; Roitman *et al.*, 2008; Rodrigues-Souza *et al.*, 2015). Consequently, we argue that the different 'spaces' adequately reflect different 'times' or levels of forest development, with varying nonlinear consequences to savanna diversity. Monitoring of fire exclusion experiments enabling a truly temporal analysis would undoubtedly add useful validity to the trends presented here.

The nature of carbon-diversity trade-offs is relevant to a number of other savanna regions threatened by woody encroachment due to either fire management or other processes. In Africa, large areas are experiencing

woody thickening, attributed to a number of factors such as increasing CO_2 and land management (Wigley *et al.*, 2010; Buitenwerf *et al.*, 2012). Similar to Brazil, fire suppression is one common candidate leading to woody thickening, either through direct reduction of fires or through increased grazing (Roques *et al.*, 2001; Higgins *et al.*, 2007). However, African savannas tend to be drier, which may limit the degree of woody encroachment and possible carbon sequestration (Staver *et al.*, 2011). In Australia, long-term changes in precipitation have been hypothesized to play a role in woody encroachment (Fensham *et al.*, 2005), but similar to both Africa and South America, fire also influences woody cover in Australia (Fensham *et al.*, 2003). Consequently, management of the fire regime is at the root of limiting woody encroachment in savannas globally (Bond *et al.*, 2005). Future studies should carefully evaluate the diversity consequences of increased woody biomass in African and Australian savannas.

In conclusion, our results illustrate that there is a large carbon-diversity trade-off between maintaining species endemic to savannas vs. promoting carbon storage. When considering all species in a plot, biodiversity increases with carbon storage in an expected manner, similar to previous studies (e.g., Gilroy *et al.*, 2014). In the Cerrado, this pattern is driven by the fact that forests have more woody species than savannas; the dramatic community replacement and subsequent exclusion of savanna endemics that occurs with carbon gains complicate the cobenefit between carbon and total biodiversity. Importantly, however, the relative carbon-diversity benefits for forest species vs. carbon-diversity trade-offs for savanna species include a point of diminishing returns, where increasing carbon will result in larger savanna species losses than gains in forest species per unit of carbon stored. The nature of this trade-off must be acknowledged in future management of this critical biodiversity hotspot.

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Supporting Information

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

Table S1. List of sites, their classification, plant species richness and total biomass.
Table S2. Model comparison results.
Table S3. Best fit model coefficients.
Table S4. Results from repeated resampling analysis.
Figure S1. Map of study sites.
Figure S2. Species accumulation curves.
Figure S3. Species richness separated by plots categorized into different biomes.
Figure S4. Shannon diversity index.
Figure S5. Pielou's evenness metric.
Figure S6. Plot of results from repeated resampling analysis.
Figure S7. Distribution of selected protected areas and potential species losses.
Figure S8. Swapping rarefaction approach.
Figure S9. Distribution of tree cover in select protected areas.