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DR. FABIO ANTONIO R MATOS (Orcid ID : 0000-0002-7699-9522)

PROF. LUIZ FERNANDO MAGNAGO (Orcid ID : 0000-0001-6335-754X)

MISS NATHALIA VIEIRA HISSA SAFAR (Orcid ID : 0000-0003-1364-4983)

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Secondary forest fragments offer important carbon-biodiversity co-benefits

Fabio A. R. Matos[1,2,3,4*], Luiz Fernando S. Magnago[5], Carlos Aquila Chan Miranda[2], Luis Fernando Tavares de Menezes[4], Markus Gastauer[6], Nathália V. H. Safar[7], Carlos Ernesto G. Reynaud Schaefer[7], Mônica P. Da Silva[8], Marcelo Simonelli[9], Felicity A. Edwards[10], Sebastião V. Martins[11], João Augusto A. Meira-Neto[1], AND David P. Edwards[2*]

[1]*Laboratory of Ecology and Evolution of Plants (LEEP), Botany graduate program (PPGBot), Departamento de Biologia Vegetal, Universidade Federal de Viçosa (UFV), Viçosa, Minas Gerais, Brazil*

[2]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, United Kingdom*

[3]*Faculdade Zacaria de Góes, Departamento de Biologia Geral, Valença, Bahia, CEP: 45.400-000, Brazil*

[4]*Universidade Federal do Espírito Santo (CEUNES / DCAB), BR 101 Norte, Km 60 - Bairro Litorâneo, São Mateus, Espírito Santo, CEP: 29.932-900, Brazil*

[5]*Universidade Federal do Sul da Bahia, Centro de Formação em Ciências e Tecnologias Agroflorestais, Ilhéus, Bahia, Brazil*

[6]*Instituto Tecnológico Vale, Rua Boaventura da Silva, 955, Bairro Umarizal, CEP: 66055-090, Belém, Pará, Brazil.*

[7]*Núcleo Terrantar, Universidade Federal de Viçosa (UFV), Viçosa, Minas Gerais,* CEP: 36570-900, *Brazil*

[8]*Instituto Federal de Educação, Ciência e Tecnologia Baiano, Departamento de Biologia Geral, Valença, Bahia, CEP: 45400-000, Brazil*

[9]*Instituto Federal do Espírito Santo, Vitória, Espírito Santo, CEP: 29056-264, Brazil*

[10]*Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YW, United Kingdom*

[11]*Forest Engineering Department, Universidade Federal de Viçosa, Avenida P. H. Rolfs s/n, CEP 36570-000 Viçosa, MG, Brazil*

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*These authors contributed equally

Corresponding authors:

Fabio A. R. Matos, *Faculdade Zacaria de Góes, Departamento de Biologia Geral, Valença, Bahia, CEP: 45.400-000, Brazil,* Tel.: +55 (75) 3643-3900; E-mail: fabiomatos.bio@gmail.com

David P. Edwards, *Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, United Kingdom,* Tel.: +44 (0)114 2220147; E-mail: david.edwards@sheffield.ac.uk

João Augusto A. Meira-Neto, *Laboratory of Ecology and Evolution of Plants (LEEP), Botany graduate program (PPGBot), Departamento de Biologia Vegetal, Universidade Federal de Viçosa (UFV), Viçosa, Minas Gerais, Brazil,* Tel.: +55 (31) 3899-1955; E-mail: j.meira@ufv.br

Authorship statement

F.A.R.M., L.F.S.M. and D.P.E. conceived the ideas and designed methodology; F.A.R.M., C.A.C.M., L.F.S.M., N.V.H.S., C.E.G.R.S., M.P.S., M.S., S.V.M., and J.A.A.M.N collected the data; F.A.R.M., M.G, and F.E. analysed the data; F.A.R.M., L.F.T.M., L.F.S.M., J.A.A.M.N., and D.P.E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Abstract

Tropical forests store large amounts of carbon and high biodiversity, but are being degraded at alarming rates. The emerging global Forest and Landscape Restoration (FLR) agenda seeks to limit global climate change by removing carbon dioxide from the atmosphere through the growth of trees. In doing so, it may also protect biodiversity as a free co-benefit, which is vital given the massive shortfall in funding for biodiversity conservation. We investigated whether natural forest regeneration on abandoned pastureland offers such co-benefits, focusing for the first time on the recovery of taxonomic, phylogenetic and functional diversity of trees, including the recovery of threatened and endemic species richness, within isolated secondary forest fragments. We focused on the globally threatened Brazilian Atlantic Forest, where commitments have been made to restore one million hectares under FLR. Three decades after land abandonment, regenerating forests had recovered ~20% (72 Mg/ha^{-1}) of the above-ground carbon stocks of a primary forest, with cattle pasture containing just

3% of stocks relative to primary forests. Over this period, secondary forest recovered ~76% of taxonomic, 84% of phylogenetic and 96% of functional diversity found within primary forests. In addition, secondary forests had on average recovered 65% of threatened and ~30% of endemic species richness of primary Atlantic forest. Finally, we find positive relationships between carbon stock and tree diversity recovery. Our results emphasize that secondary forest fragments offer co-benefits under FLR and other carbon-based payments for ecosystem service schemes (e.g. carbon enhancements under REDD +). They also indicate that even isolated patches of secondary forest could help to mitigate climate change and the biodiversity extinction crisis by recovering species of high conservation concern and improving landscape connectivity.

INTRODUCTION

Tropical forests account for ~32% of global primary production (Field, Behrenfeld, Randerson, & Falkowski, 1998), harboring the largest above-ground carbon stocks and highest levels of biodiversity. However, these regions are increasingly human-dominated (Lewis, Edwards, & Galbraith, 2015), having experienced dramatic degradation via selective logging and fire, deforestation for agriculture (more than 1.5 million km^2 between 1980 and 2012, Gibbs et al., 2010; Hansen et al., 2013), and resulting fragmentation of remaining forests (Haddad et al., 2015). Combined, these land-use changes are driving climate change, via anthropogenic carbon emissions (Van der Werf et al., 2009), and causing massive loss of global biodiversity (Pimm et al., 2014).

Under the 2014 Paris Agreement, the Parties of the United Nations Framework Convention on Climate Change (UNFCCC) agreed to use Forest and Landscape Restoration (FLR) as a central component of an integrated programme of interventions to restrict global warming to 2°C by growing trees in degraded landscapes to sequester ~1.7 gigatonnes of carbon dioxide (CO_2) equivalent annually (Gellie et al., 2018). The Bonn Challenge has seen nations agree to restore the ecological functionality of 350 million hectares of deforested and degraded land by 2030 (www.bonnchallenge.org). Furthermore, the Reducing Emissions from Deforestation and Forest Degradation (REDD+) carbon-based payments for ecosystem services mechanism includes actions that enhance forest carbon stocks, including natural regrowth. Given dramatic shortfalls in the conservation budget (McCarthy et al., 2012), an important potential is for both FLR and REDD+ to also protect biodiversity as a co-benefit without additional cost.

Above-ground biomass (AGB) recovery in secondary forests can be rapid. In lowland Neotropical secondary forests, Poorter et al., (2016) demonstrated that after 20 years since land abandonment, the carbon-absorption rate in secondary forests was 11 times the uptake rate of old-growth forests, and that AGB stocks take a median of 66 years to recover 90% of old-growth AGB levels, while in the Tropical Andes, after 30 years of secondary succession approximately half of old-growth AGB had been restored (Gilroy et al., 2014).

Within secondary forests, there can also be substantial recovery of species diversity across a range of taxa (Barlow et al., 2007), with positive co-benefits between carbon stocks and bird, dung beetle, and amphibian diversity in the Tropical Andes (Gilroy et al., 2014; Basham et al., 2016), and trees, birds and dung beetles in the Brazilian Amazon (Lennox et al., 2018; Ferreira et al., 2018). Although these studies covered a wide range of taxonomic groups, they only focused on taxonomic (species) diversity. A key question, therefore, is whether there are positive co-benefits between recovery of carbon and of phylogenetic and functional diversity.

Phylogenetic and functional diversity metrics provide important information on community responses to anthropogenic changes (Magnago et al., 2014; Matos et al., 2017). Phylogenetic diversity is based on evolutionary relationships, thus reflecting the evolutionary history of a particular community (Faith 1992; Webb, 2000). Phylogenetic diversity allows understanding of the assembly of biological communities and ecological processes, and is vital for protecting evolutionary history (Veron, Davies, Cadotte, Clergeau, & Pavoine, 2015). Functional diversity considers the functional characteristics and roles of species within a community (Petchey & Gaston, 2002; Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009), with functionally diverse communities demonstrating resilience in the functioning of ecosystems more effectively than taxonomic diversity (Magnago et al., 2014; Magnago et al., 2015).

Here, we investigate possible co-benefits between carbon and biodiversity considering the taxonomic, phylogenetic and functional diversity of trees in the globally threatened Brazilian Atlantic forest, where commitments have been made to restore one million hectares of degraded landscapes under FLR. Trees are critical for habitat structure, carbon storage, and maintenance of diversity in other groups (Banks-Leite et al., 2014). Our central questions were thus: (i) How rapidly do secondary forest fragments recover above-ground carbon in highly degraded landscapes after land abandonment? (ii) How rapidly do taxonomic, phylogenetic and functional diversity return in secondary forest fragments? (iii) How rapidly do species composition (i.e., different organisms that make up a community) and species of high conservation value (i.e., IUCN red-listed and endemic species) return in secondary forest fragments? (iv) What is the effectiveness of secondary forest fragments in providing co-benefits between carbon and tree diversity and species of high conservation value?

MATERIALS AND METHODS

Study area

Our study area was based from Espírito Santo (19°51'57.14"S and 40° 7'15.28"W) to southern Bahia (18°1'52.25"S and 39°54'41.10"W), east Brazil (Fig. 1; Supporting Information Table S1), which contains a landscape matrix composed of cattle pastures, plantations of *Eucalyptus* spp., sugar cane, coffee, and papaya, and forest fragments (Rolim, Jesus, Nascimento, do Couto, & Chambers, 2005). The prevailing climate is wet tropical (Köppen climate classification), with low rainfall from April to September followed by high precipitation from October to March, and with minimal variation in climate across sampling sites: precipitation ranges from 1,228 mm yr^{-1} in Espírito Santo (Peixoto & Gentry 1990) to ~1,403 mm yr^{-1} in Bahia (Gouvêa, 1969), with similar average temperatures in the dry season (Espírito Santo ~15.6°C; Bahia ~14°C) and the wet season (Espírito Santo ~27.4°C; Bahia ~23°C).

These forest areas are included in the Atlantic Forest domain (IBGE, 1987), typified by large flat areas rising slowly from 20 to 200 m a.s.l., and according to the Brazilian vegetation classification are Lowland Rain Forest (IBGE, 1987). The studied landscape remained well preserved until the 1950's, with Espírito Santo and Bahia subsequently experiencing rampant clear-cut logging and charcoal production, followed by agriculture (Magnago et al., 2015). The main deforestation period in our study area was thus between the 1950s and early 1970s, with conversion of forests predominantly to cattle pasture and sugar cane.

Experimental design

Fieldwork was conducted across three habitat types. 1) Primary forest - forest remnants spanning 153 to 23,480 ha (Supporting Information Table S1), occurring outside and within conservation units and with no evidence of recent logging, fire and hunting, but with large impacts via fragmentation effects in smaller patches and at edges on carbon stock, functional diversity, and species with conservation value (Magnago et al., 2014; Magnago et al., 2015); 2) Secondary forest - defined as recovering areas after total removal of trees (Corlett, 1994), sampled forests ranged from 5 to 30 years after land abandonment and 9 to 203 ha in area (Supporting Information Table S1); and 3) Cattle pasture – These were active areas of production (i.e., not abandoned), characterized by the predominant presence of pasture with isolated remaining trees. We focus on cattle farming because it represents 36% of agricultural land across Espírito Santo and Bahia (Supporting Information Table S2).

Tree sampling

For each type of habitat (i.e., primary forest, secondary and cattle pasture), 13 points were sampled, with each sampling point consisting of a transect of approximately 280 meters. On each transect, we sampled 10 plots of 10 m x 10 m (0.1 ha) located at 20 m intervals along each transect, with the plots of primary forest positioned ≥200 m from the forest edge. We thus sampled 390 plots (3.9 ha) in total, with 1.3 ha per habitat type.

Within each plot, we sampled both the shrub and arboreal strata, including all tree individuals rooted within our plots ≥4.8 cm in diameter at breast height (dbh; 1.30 meters above ground height) (following Magnago et al., 2014; Magnago et al., 2015; Matos et al., 2017). Individuals that straddled the plot edge were counted as being within the plot if at least half of the trunk was inside the plot. For tree individuals that were not identified at the site, we collected leaves and any reproductive parts, and these were then classified into morphospecies and subsequently identified by morphological comparison in the Herbarium of Vale (CVRD) or by botanical experts for their families. The botanical material collected in reproductive stage was deposited in the Herbarium of the Federal University of Viçosa, Minas Gerais (VIC) and CVRD.

Above-ground carbon stock

The above-ground biomass (AGB) of each tree was estimated using the allometric equation of Chave et al., (2014), defined as:

$$\mathrm{AGB_{est}} = \exp[-1.803 - 0.976E + 0.976\ln(\rho) + 2.673\ln(D) - 0.0299[\ln(D)]^2]$$

where $\mathrm{AGB_{est}}$ is the estimated aboveground biomass in Mg, E is a measure of environmental stress; ρ is wood density ($g.cm^{-3}$) and D (cm) is the diameter of the tree at breast height. The value for wood density in dry weight ($g\ cm^{-3}$) was obtained from Global Wood Density database (GWD) (available in: http://dx.doi.org/10.5061/dryad.234/1; Chave et al., 2009). When a species was identified at the genus level or was not present in the GWD database, we used the average density of wood for all species of the same genus in the database (Flores & Coomes, 2011; Magnago et al., 2015). All analyses to obtain biomass per tree were carried out using the BIOMASS package for R (Réjou-Méchain, Tanguy, Piponiot, Chave, & Hérault, 2017). Finally, we obtain the value of carbon for each transect of each treatment (i.e., primary forest, secondary forest, and cattle pasture), assuming that 50% of AGB of each individual is represented by carbon (Malhi et al., 2004).

Phylogenetic hypothesis

We constructed a list (i.e., family/genus/species, according to APG IV 2016; Chase et al., 2016) containing all species identified at the most specific taxonomic level (89.87% of all species sampled). This list was submitted to ComTreeOpt function to build and optimize community tree topology via Open Tree Reference Taxonomy (ComTreeOpt package para R is available on: https://github.com/iantrotter/ComTreeOpt; Gastauer, Caldeira, Trotter, Ramos, & Meira Neto, 2018). The generated phylogenetic hypothesis was calibrated using mean age estimates for internal nodes from Magallón et al., (2015), and the BLADJ algorithm in Phylocom program version 4.2 (Webb, Ackerly, & Kembel, 2008).

Traits and functional dendrogram

Functional trait matrix - We examined six traits related to: i) quantity and type of food resource (1. fruit size [mm], 2. seed size [mm], and 3. fruit type), categorized into fleshy or non-fleshy fruits; ii) fruit dispersal syndrome (4. zoochoric or non-zoochoric dispersion); iii) forest structure (5. succession group, categorized as pioneer, initial secondary or later secondary), and iv) carbon storage (6. wood density in dry weight g cm^{-3}). More details on traits selection are available in Supporting Information Text S1 (Supporting methods: Functional traits).

Functional dendrogram construction - We built one functional dendrogram containing 99% of all tree species within our habitat types using the functional characteristics within our functional trait matrix. Gower`s distance (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009) was used to create a distance matrix from continuous and categorical functional traits (See Supporting Information Text S1 for full details of functional traits), and the UPGMA clustering method. To verify the loss of information when we transformed the distance matrix into a dendrogram, we correlated the original matrix and the dendrogram cophenetic matrix; however, we did not find great loss of information (r=0.937). Lastly, we used the '*as.phylo'* function available on *ape* package to transform the functional dendrogram into a tree of class *phylo,* thus allowing the dendrogram to have the same structure as a phylogenetic tree (R Development Core Team 2018).

Diversity of trees

For taxonomic diversity (TD), species richness sampled per transect for each habitat type was used, and this measure could be interpreted as the alpha diversity for each forest remnant sampled.

Phylogenetic diversity (PD) - From our dated phylogenetic hypothesis, we calculated phylogenetic diversity using Faith's index (PD), by summing the branch lengths of the phylogenetic tree linking the species in the community, and representing the sum of evolutionary history contained in the sampled community (Faith, 1992). Since PD is correlated with species richness, we calculated the standardized effect size (sesPD) of phylogenetic diversity (Webb, 2000). The ses values measure the number of standard deviations between the observed values and expected PD (see Supporting Information Text S2 for full details). Communities with sesPD values approaching 1 (i.e., high quantiles) indicate phylogenetic evenness, or a greater phylogenetic distance among co-occurring species than expected, whereas communities with sesPD approaching 0 (i.e., low quantiles) indicate phylogenetic clustering, or smaller phylogenetic distances among co-occurring species than expected.

Functional diversity (FD) - Since a functional dendrogram has the same structure as a phylogenetic tree (Pavoine & Bonsall, 2011), we measured functional diversity as the total branch length of a functional dendrogram (Petchey & Gaston, 2002). FD frequently correlates with species richness, thus we also calculated the standardized effect size (sesFD; see Supporting Information Text S2 for full details). Communities with sesFD values approaching 1 (i.e., high quantiles) indicate functional evenness, or a greater FD distance among co-occurring species than expected, whereas communities with sesPD approaching 0 (i.e., low quantiles) indicate functional clustering, or small FD distances among co-occurring species than expected.

Species composition of trees

Overall composition and similarity to primary forest – Differences in species composition across the entire community among habitat types are not detectable using diversity measures. We thus assessed changes in community composition with a non-metric multidimensional scaling ordination (NMDS), using raw species abundance data from each transect. The NMDS analysis was performed using PAST (Version 3.21; Hammer, Haper, & Ryan, 2001), with the Bray-Curtis dissimilarity measure, and we used the scores of axis 1 and 2 of the NMDS as the measure of dissimilarity between habitat types.

Additionally, the Chao-Sørensen abundance-based similarity index (Chao, Chazdon, Colwell, & Shen, 2005) was used to evaluate the average similarity of the species composition in secondary forest (SF) and cattle pasture (CP) versus that of primary forests (PF). Average similarity was obtained using Bray-Curtis dissimilarity, thus informing how much the composition of each transect of SF and CP is similar in terms of species composition in relation to the PF (Gilroy et al., 2014). This analysis was developed in EstimateS version 9.1.0 (Colwell., 2013).

Tree conservation value – We considered the following metrics of conservation value: i) the number of species (i.e., species richness) threatened with extinction on the International Union for Conservation of Nature (IUCN, 2018) Red list, including those listed as vulnerable, endangered or critically endangered; and ii) the richness of endemic species of the Atlantic Forest. To classify the endemic species of the Atlantic forest domain, we used the database of Flora do Brasil (for more details see: https://bit.ly/2G1W2D2).

Characteristics of secondary forests

To evaluate the effect of regenerating forest characteristics on diversity and species composition metrics, we used four measures: i) patch isolation from the nearest fragment (PI), measured in meters; ii) isolation of secondary forests from fragments ≥500 ha (SD), measured in Km; iii) patch size (PS), measured in hectares, because larger patches tend to harbour more diversity and carbon stocks (Magnago et al., 2014; Magnago et al., 2015); and iv) patch age (PA), measured in years after the abandonment of the land, since secondary forests have improved biodiversity and carbon stocking overtime (Gilroy et al., 2014; see Supporting Information Table S1 for the values of each characteristic).

Except for PA, these metrics were obtained using the vegetation map of the Brazilian Atlantic forest (reference year 2016; www.sosma.org.br and www.inpe.br), on Geographic Information System QGIS 2.18.4 (QGIS Development Team, 2017). Time since land abandonment (i.e., PA) was traced using open access satellite images of surface reflectance with 30 m resolution since 1984 (LANDSAT TM4, 5-7; U.S.Geological Survey and NASA). Raw satellite layers were concatenated in a unique consensus layer (bandsetting) using a Semi-Automatic Classification Plugging function. This function automatically splits a multiband raster to single bands, which are easier to classify and then manipulate. Analysis of surface layers was again performed in the Geographic Information System QGIS 2.18.4 (QGIS Development Team, 2017).

Statistical analyses

We first use the Moran's I test to check for potential influence of spatial autocorrelation of the biotic (i.e. carbon, diversity and composition) response’s variables. Significance of Moran's test was determined by the Monte-Carlo permutation test (1000 permutations), using the R library spdep (Bivand & Piras., 2015). We found that sites are not related by their geographic position (i.e. spatial autocorrelation), both when we considered the variable responses to habitat type (i.e., primary forest, secondary forest and cattle pasture), and to the secondary forest characteristics (Supporting Information Table S3).

We used generalized linear models (*GLMs*) to investigate variation between primary, secondary and cattle pasture habitats on the biotic variables. After the construction of each model, we checked model residuals for normality and homoscedasticity, and the probability of significance (*p*-values) for each model was determined by comparing the model containing type of habitat versus the null model, using the function anova from *stats* package in R. We estimated the significance of pairwise differences between habitat effects using Tukey post-hoc tests in the multcomp on R package (Hothorn et al., 2017). The NMDS of species communities between habitat types was compared by means of the Bray-Curtis index and via an analysis of similarity (ANOSIM). The post-hoc permutation test with 999 replications was then run to detect which pairs of habitats differed. The community analysis was performed using PAST (Version 3.21; Hammer, Harper, & Ryan, 2001).

To assess the effect of secondary forest characteristics (i.e. PI, SD, PS and PA) on biotic variables, we used an information-theoretic approach and multi-model inference (Burnham, Anderson & Huyvaert, 2011). Before constructing the models, we used the package PerformanceAnalytics' in R to evaluate the correlation between the characteristics of secondary forest, and we found predictor characteristics were highly correlated ($r>0.7$; see Supporting Information Fig. S1). Thus, we constructed separate models for each variable, contrasted in each case with a null model containing only the intercept. Using the MuMIn package (Barton, 2019), we calculated Akaike's information criterion of second order (AICc indicated for small sample sizes), by the combination of all candidate models. After inspection of the models, we adopted $\Delta\text{AICc}\leq 5$ for the calculation of the average models considering that they have a lot of explanatory power and biological significance (Burnham

& Anderson, 2002). Finally, for each average model, the importance value of each predictor variable was obtained from the sum of Akaike weights (Burnham, Anderson & Huyvaert, 2011). We applied *GLMs* to evaluate co-benefits between the carbon stock of second-growth forest and diversity metrics (TD, PD, FD), community composition, and species richness with conservation value. After the construction of each model, we checked model residuals for normality and homoscedasticity. Our *GLMs* used Gaussian error and an identity link (normality was tested and confirmed by the Shapiro Wilk test), implemented in the 'glm' function from *stats* package in R, aside for count data that did not meet the assumptions of normality, for which we used a Poisson error distribution.

RESULTS

Impacts of secondary forest on carbon stocks

Across all habitat types, remnants of primary forests contained the highest average carbon stock (369.25±256.54 Mg ha^{-1} in), followed by secondary forests (26.80±19.40 Mg ha^{-1}), and then by cattle pasture (11.85±24.78 Mg ha^{-1}) (Fig. 2a). The carbon stock was significantly related with habitat type ($F_{(2,36)}=41.65$, $p<0,001$), with pairwise comparisons revealing significant differences between all habitat pairs (Fig. 2a; Supporting Information Table S4). Considering the impact of secondary forest characteristics, we found a significant negative effect of patch isolation-PI ($\beta= -0.64\pm0.14$ SE, $z= 4.54$, $p<0.001$) and source distance-SD ($\beta= -0.67\pm0.12$ SE, $z= 5.43$, $p<0.001$) on carbon stocking (Fig. 2b; Supporting Information Tables S5 and S6). Patch size-PS ($\beta= 0.64\pm0.13$ SE, $z= 4.66$, $p<0.001$) and patch age-PA ($\beta= 0.65\pm0.13$ SE, $z= 4.83$, $p<0.001$) both revealed a significant positive effect on carbon stocks (Fig. 2b; Supporting Information Tables S5 and S6). In order of independent contribution, the predictive variables that best explained changes in carbon stock were SD, followed by PA, PS and PI (Supporting Information Fig. S2a).

Impacts of secondary forest on diversity of trees

Taxonomic diversity (TD) – Across all habitats, 3330 tree individuals of 440 species were recorded. Primary forest had the highest average TD (74.07±9.34), followed by secondary forest (27.30±19.40) and cattle pasture (2.30±0.46). There was a significant effect of habitat type ($F_{(2,36)}$=148.94, p<0,0001), with pairwise comparisons revealing significant differences between all habitat pairs (Fig. 3a; Supporting Information Table S7). For the characteristics of secondary forests, we found a significant negative effect of patch isolation-PI on TD (β= -0.63±0.20 SE, z= 3.03, *p*<0.001), whereas we found a significant positive effect of patch size-PS (β= 0.65±0.19 SE, z= 3.28, *p*<0.001) and patch age-PA (β= 0.60±0.21 SE, z= 2.77, *p*<0.001) on TD (Fig. 3b; Supporting Information Tables S8 and S9). In order of independent contribution, variables that best predicted changes in TD were PS, followed by PI and PA (Supporting Information Fig. S2b).

Phylogenetic diversity (PD) - PD was related with habitat type ($F_{(2,36)}$=154.44, p<0,0001), with higher PD in primary than in secondary forests, which in turn had higher PD than did cattle pasture (Fig. 3c; Supporting Information Table S10). Considering the impact of secondary forest characteristics, we found a significant negative effect of patch isolation-PI (β= -0.39±0.09 SE, z= 4.35, *p*<0.001) and a significant positive effect of patch size-PS (β= 0.41±0.08 SE, z= 5.10, *p*<0.001) and patch age-PA (β= 0.38±0.09 SE, z= 3.9, *p*<0.001) on PD (Fig. 3d; Supporting Information Tables S11 and S12). In order of independent contribution, the variables that best predicted changes in PD were PS, followed by PI and PA (Supporting Information Fig. S2c). After correction of the relationship between PD and species richness, we found that standardized effect size of PD (sesPD) was also related with habitat type ($F_{(2,36)}$=5.397, p<0,008), revealing significantly higher phylogenetic dispersion for secondary forests and pastures than for primary forests (Fig. 3e; Supporting Information Table S10). We did not find a significant effect of patch isolation (β= 0.07±0.07 SE, z= 0.95,

p>0.05), source distance (β= 0.09±0.07 SE, z = 1.23, p>0.05), patch size (β= -0.07±0.07 SE, z = 0.93, p>0.05) or patch age (β= 0.08±0.07 SE, z = 1.11, p>0.05) on sesPD (Fig. 3f; Supporting Information Tables S11 and S12).

Functional diversity (FD) – FD was strongly related with habitat type ($F_{(2,36)}$=200.33, p<0,0001), with significant higher FD in primary than secondary forest, and in turn, in secondary forest than cattle pasture (Fig. 3g; Supporting Information Table S13). For the characteristics of secondary forests, we found a significant negative effect of patch isolation-PI (β= -0.19±0.05 SE, z= 3.40, p<0.001), whereas we found a significant positive effect of patch size-PS (β= 0.20±0.05 SE, z = 3.92, p<0.001) and patch age-PA (β= 0.19±0.05 SE, z = 3.34, p<0.001) on FD (Fig. 3h; Supporting Information Tables S14 and S15). In order of independent contribution, the variables that best predicted changes in FD were PS, followed by PI and PA (Supporting Information Fig. S2d). After correction of the relationship between FD and species richness, we found that standardized effect size of FD (sesFD) was also related with habitat type ($F_{(2,36)}$=5.397, p<0,008), revealing significantly higher phylogenetic dispersion for secondary forests and pastures than for primary forests (Fig. 3i; Supporting Information Table S13). We did not find a significant effect of patch isolation (β= 0.04±0.09 SE, z = 0.45, p>0.05), source distance (β= 0.02±0.09 SE, z = 0.31, p>0.05), patch size (β= -0.01±0.09 SE, z = 0.15, p>0.05) and patch age (β= -0.006±0.9 SE, z = 0.06, p>0.05) on sesFD (Fig. 3j; Supporting Information Tables S14 and S15).

Impacts of secondary forest on species composition

Overall composition and similarity to primary forest – There was a significant difference in species composition between habitats (ANOSIM, R=0.544; p=0.0001, Fig. 4a), with pairwise comparisons revealing significant differences between all pairs (all p=0.0001). Considering the impact of secondary forest characteristics, we found a significant negative effect of patch isolation-PI (β= -0.02±0.11 SE, z= 2.12, p<0.001) and a significant positive effect of patch size-PS (β= 0.03±0.13 SE, z= 2.35, p<0.001) and patch age-PA (β= 0.03±0.12 SE, z= 2.59, p<0.001) on NMDS-axis 1 (Fig. 4b; Supporting Information Tables S16 and S17). We found no effect of the patch characteristics on NMDS-axis 2 (e.g. all values of adjusted SE overlapping zero and p>0.05; Supporting Information Tables S16 and S17). In order of independent contribution, the variables that best predicted changes in NMDS-axis 1 were PA, followed by PS, and PI (Supporting Information Fig. S2e).

Secondary forest increased to ~44% of the average similarity of primary forests, presenting a significant relation between similarity to primary forests and habitat type ($F_{(2,36)}$=207.49, p<0,001), with secondary forests showing higher average similarity with primary forests (0.092±0.068) than did cattle pasture (0.025±0.029). Pairwise comparisons revealed significant differences between all habitat pairs (Fig. 4c; Supporting Information Table S18). For the characteristics of secondary forests, we found a significant negative effect of patch isolation-PI (β= -0.63±0.20 SE, z= 3.03, p<0.001) and a significant positive effect of patch size-PS (β= 0.65±0.19 SE, z= 3.28, p<0.001) and patch age-PA (β= 0.60±0.21 SE, z= 2.7, p<0.001) on similarity to primary forest (Fig. 4d; Supporting Information Tables S19 and S20). In order of independent contribution, the variables that best predicted changes in similarity to primary forest were PS, followed by PI, and PA (Supporting Information Fig. S2f).

Tree conservation value – The richness of IUCN Red-listed species was related with the habitat type ($\chi^2_{(2, 36)}$=141.47, p<0.001), with primary and secondary forests containing higher richness than did cattle pasture. Pairwise comparisons revealed significant differences between all habitat pairs (Fig. 4e; Supporting Information Table S21). Considering the impact of secondary forest characteristics, we found a significant negative effect of patch isolation-PI (β= -0.53±0.19 SE, z= 2.72, p<0.007) and source distance-SD (β= -0.48±0.21 SE, z= 2.25, *p*<0.003), and a significant positive effect of patch size-PS (β= 0.49±0.16 SE, z = 2.99, *p*<0.03) and patch age-PA (β= -0.52±0.20 SE, z= 2.60, *p*<0.001) on richness of IUCN Red-listed species (Fig. 4f; Supporting Information Tables S22 and S23). In order of independent contribution, the variables that best predicted changes in the IUCN Red-listed species were PS, followed by PI, PA and SD (Supporting Information Fig. S2g).

The richness of Atlantic forest endemics revealed significant relation with habitat type ($F_{(2,36)}$=279.45, p<0,0001), with primary and secondary forests harboring higher richness than cattle pasture. Pairwise comparisons revealed significant differences between all habitat pairs (Fig. 4g; Supporting Information Table S24). For the characteristics of secondary forests, we found a significant negative effect of patch isolation-PI (β= -0.66±0.14 SE, z= 0.24, *p*<0.007) and source distance-SD (β= -0.56±0.27 SE, z= 2.06, *p*<0.03), and a significant positive effect of patch size-PS (β= 0.69±0.23 SE, z = 2.92, *p*<0.003) and patch age-PA (β= -0.60±0.26 SE, z= 2.3, *p*<0.02) on richness of endemics species (Fig. 4h; Supporting Information Tables S25 and S26). In order of independent contribution, the variables that best predicted changes in the richness of endemics species were PS, followed by PI, PA and SD (Supporting Information Fig. S2h).

Co-benefits between carbon stock and tree diversity and composition

We found significant positive impacts of above-ground carbon stock recovery on all three levels of tree diversity: TD (t=7.42, *p*=0.0001; Fig. 5a); PD (t=7.03, *p*=0.0001; Fig. 5b); and FD (t=5.01, *p*=0.0003; Fig. 5c). We did not find a significant pattern for sesPD (t=-1.37, *p*=0.19) or sesFD (t=-0.37, *p*=0.71). There were also significant positive impacts of carbon stock on metrics of species composition: similarity to primary forests (t=7.19, *p*=0.0001; Fig. 5d); Red-listed species richness (t=8.23, *p*=0.0001; Fig. 5e); and Atlantic forest endemic species richness (t=5.97, *p*=0.0001; Fig. 5f).

DISCUSSION

We urgently need to seek mechanisms that can simultaneously protect both carbon and biodiversity (McCarthy et al., 2012). Here, we investigated whether regeneration of secondary forest fragments offer such co-benefits, focusing on the Brazilian Atlantic forest, where one million hectares are to be restored under FLR. While primary forests remain irreplaceable for biodiversity conservation (Gibson et al., 2011), our study highlights the important potential of secondary forests in regenerating carbon and biodiversity co-benefits. Over a period of ~30 years, a significant amount of carbon was stored and high taxonomic, phylogenetic and functional diversity of trees recovered, including threatened and endemic species, was recovered. Benefits were improved in patches suffering from less landscape-level isolation, in larger secondary forest patches, as well as with increasing patch age. Resulting positive relationships between carbon stock and tree diversity and community recovery suggest strong potential for co-benefits of natural forest regeneration under FLR and other programs, including carbon enhancements under REDD+.

Carbon stock recovery

After three decades since land abandonment, secondary forests had 72 Mg ha^{-1} of above-ground carbon, ~20% of primary forest levels (Fig. 2a). This represents a lower rate of carbon sequestration than in other tropical secondary forests. For examples, in an analysis of 1,500 carbon plots across the lowland Neotropics, Poorter et al., (2016) found an average recovery of 122 Mg/ha^{-1} (range 20 to 225 Mg/ha^{-1}) after 20 years of regeneration, while in the Tropical Andes, natural regeneration on cattle pasture resulted in ~130 Mg/ha^{-1} of above-ground carbon stocks after 30 years (Gilroy et al., 2014).

Isolation likely explains our lower rates of carbon accumulation (Fig. 2b; Supporting Information Fig. S2a). Most secondary forest plots in Poorter et al., (2016) and all of those in Gilroy et al., (2014) were connected to mature secondary or old-growth forest, whereas in this study, all secondary patches were isolated from primary forest fragments by the pasture and crop matrix, with 170±106 m to the nearest neighbour and 4±2.4 km from large forest blocks (≥500 hectares). Increasing isolation from existing forest likely limits seed dispersal (Hubbell, 2001) and the recovery of carbon stocks, especially in small fragments (Magnago et al., 2015). Additionally, the relatively small sizes of our secondary forest patches (9-203 ha, Table S1), and thus their high levels of associated edge effects (e.g. Laurance et al., 2002), also likely reduced the recovery of carbon stocks relative to larger blocks of forest (e.g. those in Gilroy et al., 2014, Poorter et al., 2016). Furthermore, the substantial defaunation in the Brazilian Atlantic forest has further potential to significantly erode seed dispersal and carbon storage (Bello et al., 2015), especially in very small and/or isolated patches (e.g. Ferraz et al., 2003).

Biodiversity recovery

In three decades of natural regeneration, secondary forests recovered ~76% of TD, 84% of PD and 96% of FD found in primary forest. The recovery of taxonomic, phylogenetic and functional diversity mirrors that of previous studies elsewhere in the Neotropics. For example, multiple taxa recovered high taxonomic diversity in the Brazilian Amazon (Barlow et al., 2007). Additionally, Edwards et al., (2017) found high recovery of PD for bird communities in the tropical Andes, while Lohbeck et al., (2012) found high recovery of FD for tree communities in Mexico. Furthermore, recovery of FD appears to be proportionally more rapid than that of TD, suggesting that systems can restore core functional roles – likely provided by functionally dominant species – even when a component of species diversity is still missing (Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016). Changes in diversity are likely to have occurred in response to changes in abiotic conditions, which become more favourable as canopy cover is restored (Senior, Hill, González Del Pliego, Goode, & Edwards, 2017). This possibility is reinforced by the fact that the increased size of secondary forest areas after land abandonment generates a significant and positive increase in diversity (Fig. 3b, d, h; Supporting Information Fig. S2b-d), and thus makes larger fragments less edge affected (Laurance et. al., 2002).

High PD recovery can be explained by two processes: the increase in TD over time or species replacements that increase the phylogenetic distance between community members (Frishkoff et al., 2014). After correcting the correlation between species richness and PD (sesPD) and FD (sesFD), secondary forests had greater phylogenetic and functional dispersion than found in primary forests (Fig. 3e,i). Higher sesPD in secondary forests thus suggests an increase of PD due to shifts in species composition towards, on average, less related species via losses of phylogenetically related species and/or gains of phylogenetically distant species, regardless of species richness (Edwards, Massam, Haugaasen, & Gilroy, 2017). The higher sesFD in secondary forests indicates lower levels of functional redundancy than observed for primary forests (Laliberté et al., 2010). Additionally, we found that the characteristics of secondary forests (i.e., PI, SD, PS and PA) had no effect on the values of sesPD and sesFD (Fig. 3f,j), which suggests that other characteristics of secondary forests or the species within the local pool influence the increase of phylogenetic and functional dispersal after land abandonment.

We also found significant recovery of tree species composition towards primary forest levels, including a host of threatened and endemic species. The amount of compositional recovery in the Amazon was much higher than documented in this study, again indicating important effects of larger patch size, of greater time since recovery (40 not 30 years) and reduced isolation (forest remnants were a median of 310 m [range 28m – 3 km] from primary forest) on floral recovery (Lennox et al., 2018). Nevertheless, our findings also suggest a high capacity of these forests to recover species of high conservation value, supporting findings for other taxa (Gilroy et al., 2014, Basham et al., 2016). This is an especially important finding given that the Brazilian Atlantic rainforest currently has ~11% of its original forest coverage, much of which is distributed in fragments smaller than 50 ha and surrounded by agricultural areas (Ribeiro et al., 2009). In combination, these results suggests that if secondary forest is recovered over much larger areas, perhaps via support from FLR and/or REDD+ (see below), then there is the potential for improved landscape connectivity and reduced extinction risk of threatened and endemic tree species (Fig. 4f,h; Supporting Information Fig. S2g,h). This would be particularly likely if secondary forest recovery also resulted in increased occurrences of fauna that play important ecological dispersal services, such as birds, dung beetles, bats, and large mammals (Barlow et al., 2007).

A caveat of our study is that the biodiversity and conservation values of our secondary forest patches are contrasted against fragmented primary forest controls that suffer edge effects (Magnago et al., 2014) and are isolated due to the low level of original forest cover (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Such primary patches are likely to have suffered fragmentation-driven losses in their tree communities (e.g. Laurance et al., 2002) and thus there is a risk that rather than our results representing a high level of resilience within this ecosystem, our control primary patches represent a shifted baseline. Such a substantially lowered comparative benchmark could make our secondary patches appear to have higher rates of recovery than would occur if contrasted against contiguous primary forests. That said, given that the entire Brazilian Atlantic forest now lacks contiguous lowland forest, and that we found substantial recovery of endemic species and those at high risk of extinction in our secondary patches, our results point towards an important conservation role for secondary forests.

Carbon and biodiversity co-benefits

We found positive relationships between carbon stock and taxonomic, phylogenetic and functional diversity, as well as community similarity to primary forests, and IUCN Red-listed and endemic species richness (Fig. 5). These findings suggest strong potential for co-benefits via carbon enhancements under natural forest regeneration in the Brazilian Atlantic for trees, similar to those identified in secondary forests of the Tropical Andes for birds, dung beetles and amphibians (Gilroy et al., 2014; Basham et al., 2016), and within degraded forests for birds, dung beetles and trees within the Brazilian Amazon (Lennox et al., 2018).

The majority of carbon-based payments for ecosystem services are unlikely to offer payments to directly conserve biodiversity (Phelps, Webb, & Adams, 2012). Rather, market forces will likely seek the cheapest options for forest restoration and associated carbon recovery. In the Tropical Andes, for example, very low economic returns from farming and rapid carbon recovery in pastures adjacent to contiguous primary forest make it relatively cheap (~\$2 t^{-1} CO_2) to promote carbon enhancements (Gilroy et al., 2014). Although we found significant recovery of carbon in landscapes with highly isolated patches of secondary forest in the Brazilian Atlantic, these rates of recovery were relatively low (Gilroy et al., 2014; Poorter et al. 2016; Lennox et al., 2018). This could result in higher carbon prices of secondary regrowth in locations isolated from primary forest blocks (Busch et al., 2019).

CONCLUSIONS

Reducing anthropogenic climate change and tropical biodiversity loss are two of the greatest challenges facing humanity (Barnett & Adger, 2007; Turner, Oppenheimer, & Wilcove, 2009; Cardinale et al., 2012). One possibility is to tackle these challenges jointly under FLR and REDD+. Our results revealed positive carbon-tree diversity co-benefits in regenerating secondary forests from highly degraded and fragmented landscapes in the globally threatened Brazilian Atlantic forest. This underscores the importance of focusing more carbon sequestration and conservation efforts on enhancing the rate with which marginal land is abandoned even, or perhaps especially, within very fragmented forest biomes. Of particular importance from a biodiversity conservation perspective is the potential for secondary forests to enlarge the area of existing fragments of primary forest (Poorter et al. 2016; Gilroy et al., 2014) and, as suggested by the substantial recovery of threatened and endemic tree species within less isolated secondary forest fragments, to improve landscape connectivity (Metzger et al. 2009) and reduce extinction risk.

Enhancing the rate of land abandonment may entail land purchase or renting (under long-term certified emissions reductions lCER schemes; Gilroy et al., 2014) to allow the regrowth of secondary forest, provided that programs ensure full prior and informed consent from land-owners. In much of the Tropical Andes, for example, it would be more profitable to grow carbon than cows (Gilroy et al., 2014). Because we found relatively low rates of carbon sequestration in our secondary forest fragments that were isolated from primary forest sources, the best option may be to focus restoration and carbon projects next to (or very near to) smaller patches with specific conservation-values and larger primary forest blocks. In such instances, they would buffer and enlarge these areas, likely reducing extinction risk. A key remaining question is whether such a strategy would also offer cheaper carbon pricing. Via improved dispersal opportunities, there would likely be higher rates of carbon recovery and this suggests that carbon prices could be lower, making them a more attractive win-win for climate change mitigation and biodiversity conservation.

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Fig. 1. Study area sampled in the Brazilian Atlantic Forest. Additional information about each transect sampled can be found in Supporting Information Table S1.

Fig. 2. Impact of habitat type and of patch isolation, size and age on carbon stocks. a) Carbon stock between primary and secondary forest, and cattle pasture. Different letters indicate significance at $p \leq 0.05$, and errors bars represent standard error. b) Effect of patch characteristics of secondary forests on carbon stocks: PI = patch isolation from the nearest fragment; SD = isolation from fragments ≥500 ha; PS = patch size; and PA = patch age. The positive or negative position of the bars represents an effect of the predictive variable on carbon stocks, and errors bars represent the (±) adjusted standard errors obtained after analysis of average models. The analysis of average models was performed considering all the models with values of ΔAICc≤ 5.

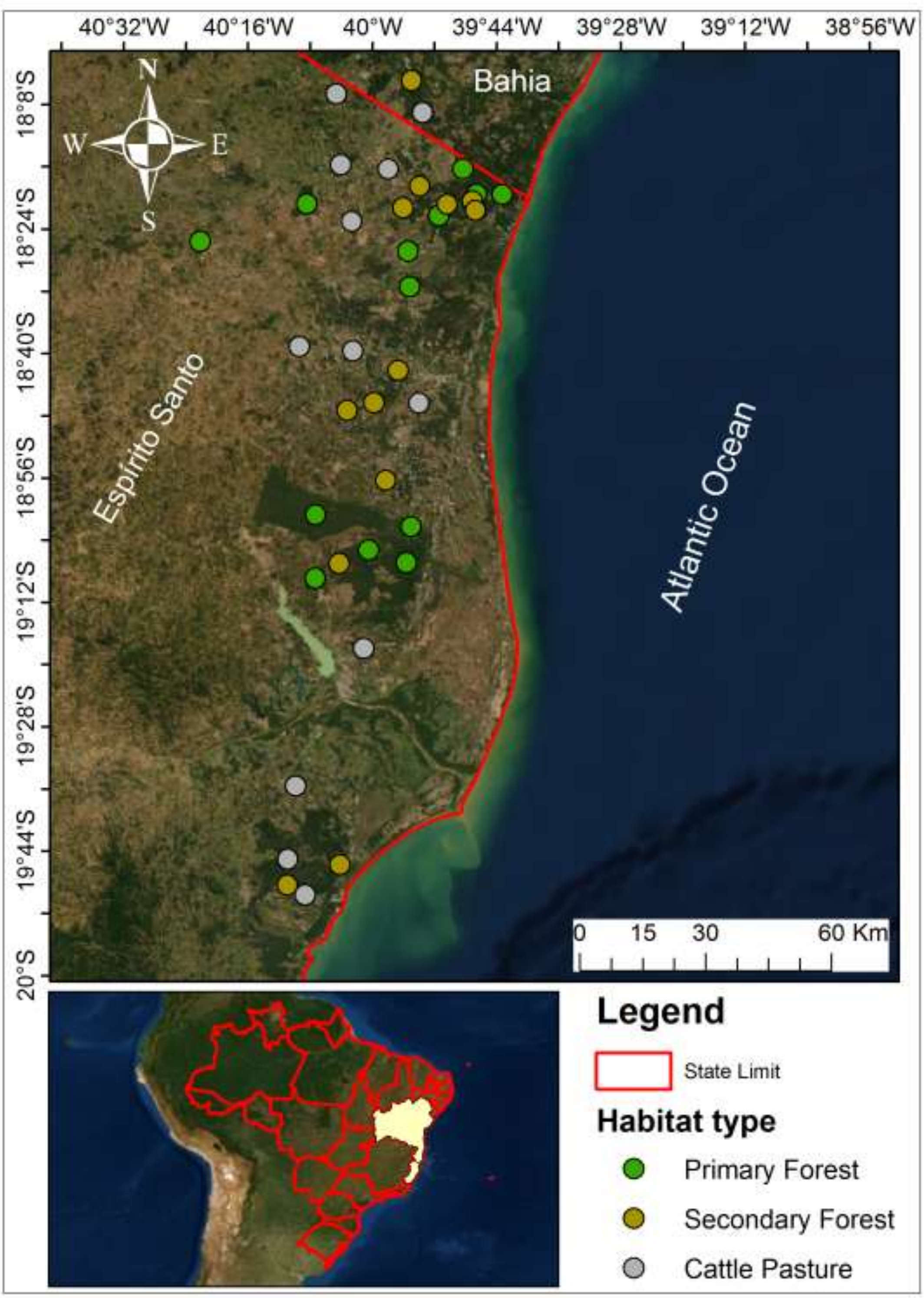
Fig. 3. Impact of habitat type (a, c, e, g, i) and of patch isolation, size, and age (b, d, f, h, j) on tree diversity. a) Taxonomic diversity (TD; i.e., species richness) between primary forest, secondary forest and cattle pasture. Different letters indicate significance at $p \leq 0.05$, and errors bars represent standard error. b) Effect of patch characteristics of secondary forests on TD. PI= patch isolation from the nearest fragment; SD= patch isolation from fragments ≥500 ha; PS = patch size; and PA = patch age. The positive or negative position of the bars represents an effect of the predictive variable on the response variable, and errors bars represent the (±) adjusted standard errors obtained after analysis of average models. The analysis of average models was performed considering all the models with values of ΔAICc≤ 5. c) Phylogenetic diversity (PD) in millions of years between habitat types; d) effect of patch characteristics of secondary forests on PD; e) standard effect size of PD (sesPD) between habitat types; f) effect of patch characteristics of secondary forests sesPD; g) functional

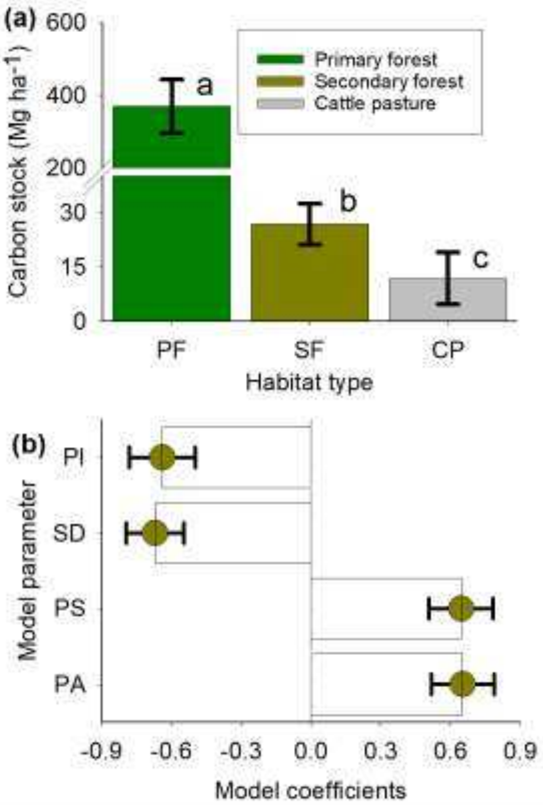
diversity (FD) between habitat types; h) effect of patch characteristics of secondary forests on FD; i) standard effect size of functional diversity (sesFD) between habitat types; and j) effect of patch characteristics of secondary forests on sesFD.

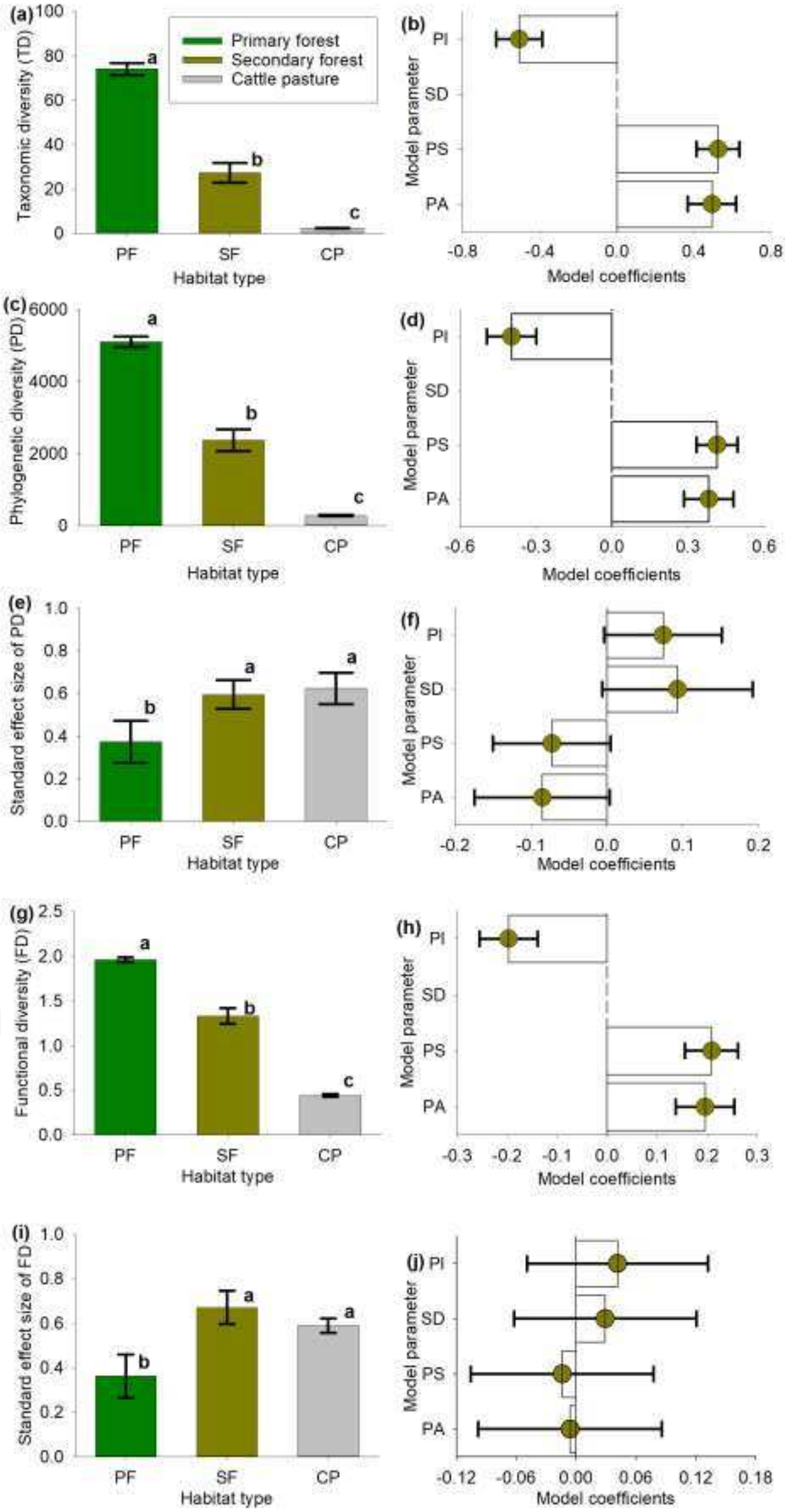
Fig. 4. Impact of habitat type (a, c, e, g) and of patch isolation, size, and age (b, d, f, h) on species composition. a) Non-metric multidimensional scaling (NMDS) ordination of community structure between primary forest, secondary forest and cattle pasture; b) effect of patch characteristics of secondary forests on tree community (NMDS axis 1): PI = patch isolation from the nearest fragment; SD = isolation from fragments ≥500 ha; PS = patch size; and PA = patch age. The positive or negative position of the bars represents an effect of the predictive variable on the response variable, and errors bars represent the (±) adjusted standard errors obtained after analysis of average models. The analysis of average models was performed considering all the models with values of ΔAICc≤ 5. c) Similarity to primary forest between habitat types. Different letters indicate significance at $p \leq 0.05$ and errors bars represent standard error. d) Effect of patch characteristics of secondary forests on similarity to primary forest; e) richness of threatened tree species among habitat types; f) effect of patch characteristics of secondary forests on richness of threatened tree species; g) richness of Atlantic forest endemic species between habitat types; and h) effect of patch characteristics of secondary forests on richness of endemic species.

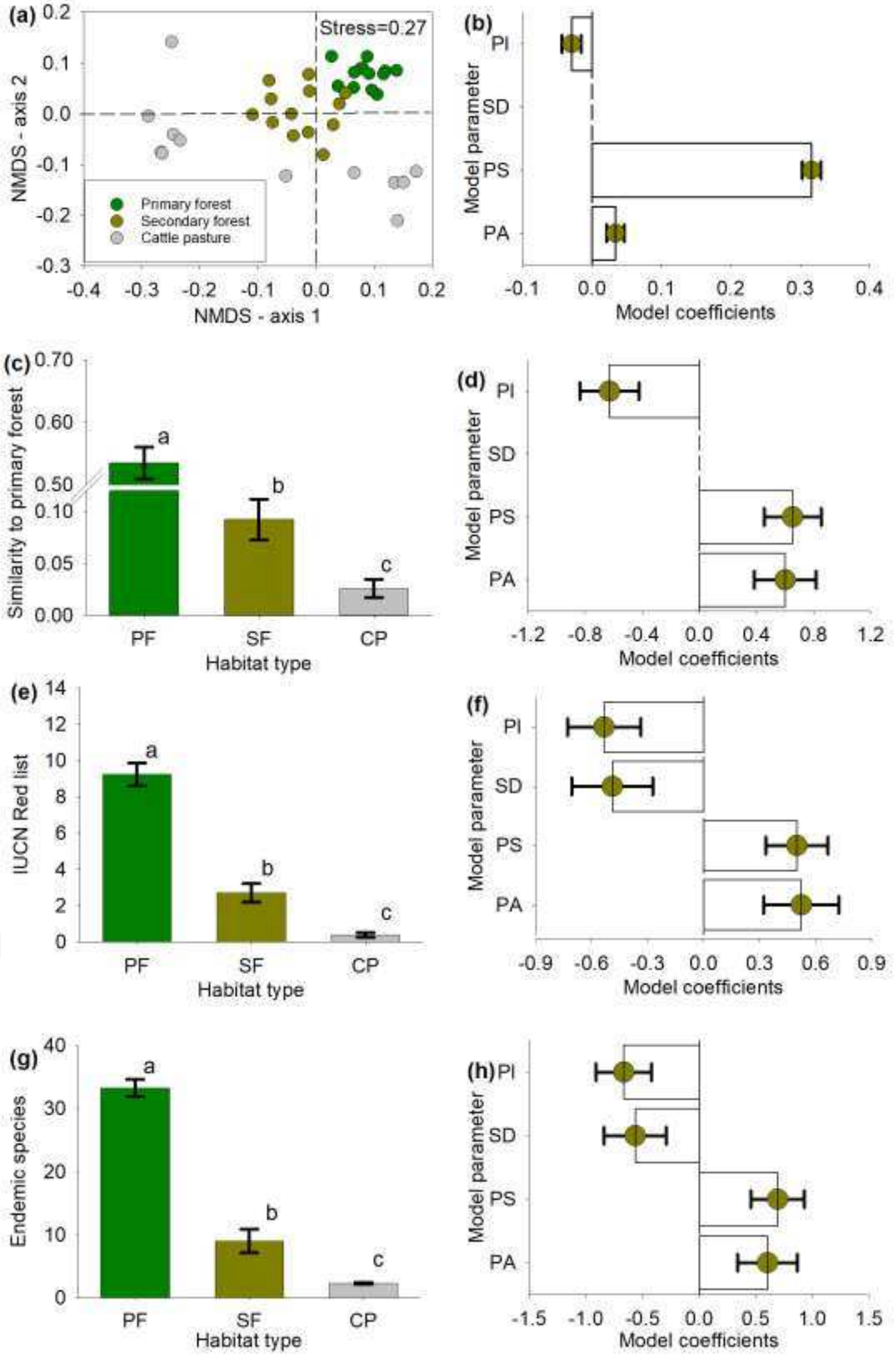
Fig. 5. Co-benefits between carbon stock and tree diversity (a-c) and composition (d-f) in the globally threatened Atlantic Forest. a) Taxonomic diversity; b) phylogenetic diversity, in millions of years; c) functional diversity; d) similarity to the primary forest community; e) species richness of trees threatened with extinction (IUCN Red listed); and f) species richness

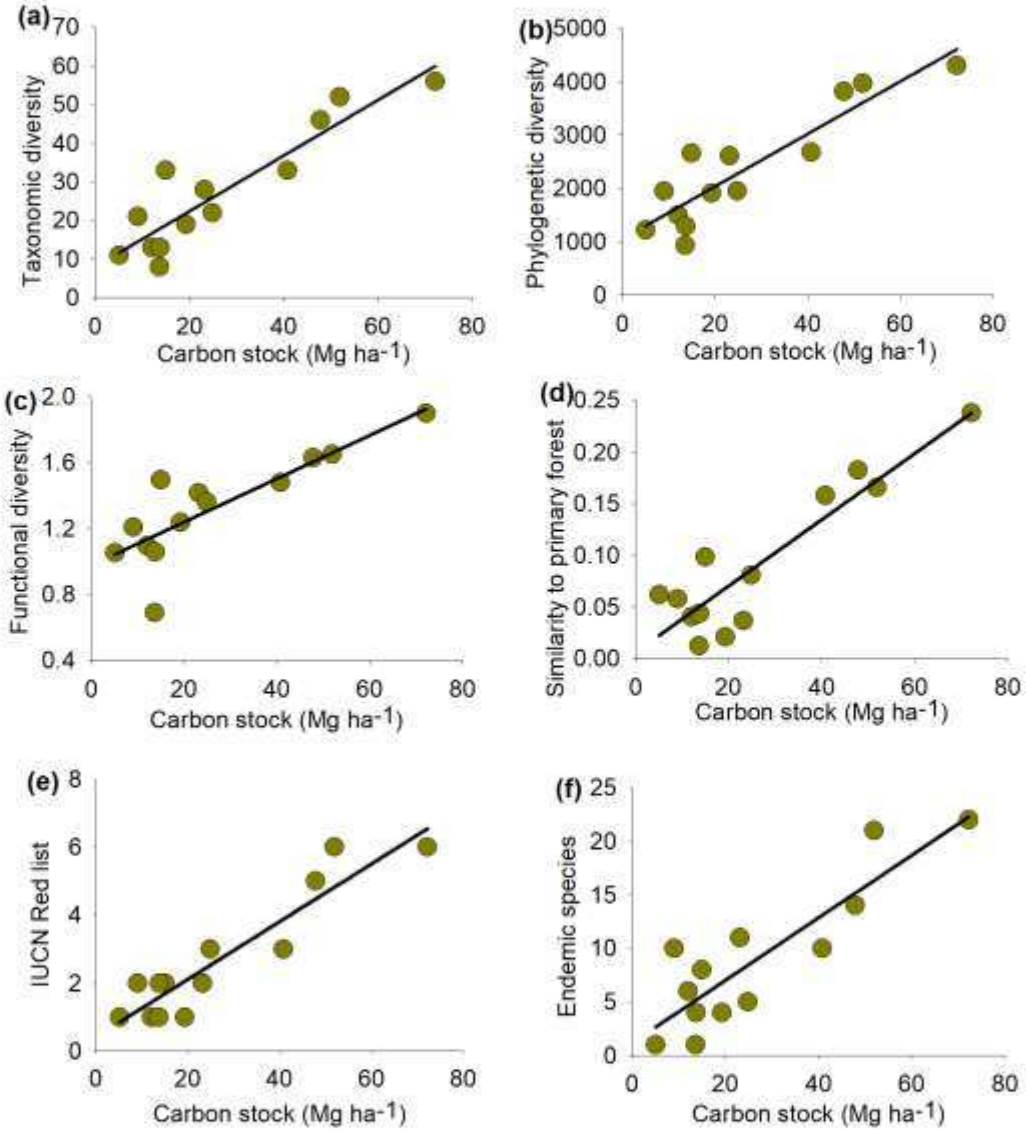
of Atlantic forest endemic trees. Additional information about results of analysis can be found in Supporting Information Table S27.




(a)
600
400
200
30
15
0
Carbon stock (Mg ha-1)
Primary forest
Secondary forest
Cattle pasture
a
b
c
PF
SF
CP
Habitat type
(b)
PI
SD
PS
PA
Model parameter
-0.9
-0.6
-0.3
0.0
0.3
0.6
0.9
Model coefficients


(a)
Taxonomic diversity (TD)
100
80
60
40
20
0
a
b
c
PF
SF
CP
Habitat type
Primary forest
Secondary forest
Cattle pasture
(b)
Model parameter
PI
SD
PS
PA
-0.8
-0.4
0.0
0.4
0.8
Model coefficients
(c)
Phylogenetic diversity (PD)
6000
4000
2000
0
a
b
c
PF
SF
CP
Habitat type
(d)
Model parameter
PI
SD
PS
PA
-0.6
-0.3
0.0
0.3
0.6
Model coefficients
(e)
Standard effect size of PD
1.0
0.8
0.6
0.4
0.2
0.0
b
a
a
PF
SF
CP
Habitat type
(f)
Model parameter
PI
SD
PS
PA
-0.2
-0.1
0.0
0.1
0.2
Model coefficients
(g)
Functional diversity (FD)
2.5
2.0
1.5
1.0
0.5
0.0
a
b
c
PF
SF
CP
Habitat type
(h)
Model parameter
PI
SD
PS
PA
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
Model coefficients
(i)
Standard effect size of FD
1.0
0.8
0.6
0.4
0.2
0.0
b
a
a
PF
SF
CP
Habitat type
(j)
Model parameter
PI
SD
PS
PA
-0.12
-0.06
0.00
0.06
0.12
0.18
Model coefficients


(a)
Stress=0.27
NMDS - axis 2
NMDS - axis 1
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
Primary forest
Secondary forest
Cattle pasture
(b)
PI
SD
PS
PA
Model parameter
-0.1
0.0
0.1
0.2
0.3
0.4
Model coefficients
(c)
Similarity to primary forest
0.70
0.60
0.50
0.10
0.05
0.00
a
b
c
PF
SF
CP
Habitat type
(d)
PI
SD
PS
PA
Model parameter
-1.2
-0.8
-0.4
0.0
0.4
0.8
1.2
Model coefficients
(e)
IUCN Red list
14
12
10
8
6
4
2
0
a
b
c
PF
SF
CP
Habitat type
(f)
PI
SD
PS
PA
Model parameter
-0.9
-0.6
-0.3
0.0
0.3
0.6
0.9
Model coefficients
(g)
Endemic species
40
30
20
10
0
a
b
c
PF
SF
CP
Habitat type
(h)
PI
SD
PS
PA
Model parameter
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Model coefficients


(a)
Taxonomic diversity
0
10
20
30
40
50
60
70
0
20
40
60
80
Carbon stock (Mg ha-1)
(b)
Phylogenetic diversity
0
1000
2000
3000
4000
5000
0
20
40
60
80
Carbon stock (Mg ha-1)
(c)
Functional diversity
0.4
0.8
1.2
1.6
2.0
0
20
40
60
80
Carbon stock (Mg ha-1)
(d)
Similarity to primary forest
0.00
0.05
0.10
0.15
0.20
0.25
0
20
40
60
80
Carbon stock (Mg ha-1)
(e)
IUCN Red list
0
2
4
6
8
0
20
40
60
80
Carbon stock (Mg ha-1)
(f)
Endemic species
0
5
10
15
20
25
0
20
40
60
80
Carbon stock (Mg ha-1)