

Environmental Research Letters



LETTER

Greater stability of carbon capture in species-rich natural forests compared to species-poor plantations

OPEN ACCESS

RECEIVED

7 August 2019

REVISED

5 December 2019

ACCEPTED FOR PUBLICATION

6 December 2019

PUBLISHED

18 February 2020

Original content from this work may be used under the terms of the [Creative Commons Attribution 3.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



Anand M Osuri^{1,2} , Abhishek Gopal³ , T R Shankar Raman³ , Ruth DeFries⁴ , Susan C Cook-Patton² and Shahid Naeem⁴

¹ The Earth Institute, Columbia University, New York 10027, NY, United States of America

² The Nature Conservancy, Arlington 22203, VA, United States of America

³ Nature Conservation Foundation, Mysore 570017, Karnataka, India

⁴ Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York 10027, NY, United States of America

E-mail: moanand@gmail.com

Keywords: biodiversity–ecosystem function relationship, carbon sequestration, drought, enhanced vegetation index, monoculture plantation, stability, tropical forest

Supplementary material for this article is available [online](#)

Abstract

Tree plantations and forest restoration are leading strategies for enhancing terrestrial carbon (C) sequestration and mitigating climate change. While it is well established that species-rich natural forests offer superior C sequestering benefits relative to short-rotation commercial monoculture plantations, differences in rates of C capture and storage between longer-lived plantations (commercial or non-commercial) and natural forests remain unclear. Using a natural experiment in the Western Ghats of India, where late-20th century conservation laws prohibited timber extraction from monodominant plantations and natural forests within nature reserves, we assessed forests and plantations for aboveground C storage and the magnitude and temporal stability of rates of photosynthetic C capture (gross primary production). Specifically, we tested the hypothesis that species-rich forests show greater temporal stability of C capture, and are more resistant to drought, than monodominant plantations. Carbon stocks in monodominant teak (*Tectona grandis*) and Eucalyptus (*Eucalyptus spp.*) plantations were 30%–50% lower than in natural evergreen forests, but differed little from moist-deciduous forests. Plantations had 4%–9% higher average C capture rates (estimated using the Enhanced Vegetation Index–EVI) than natural forests during wet seasons, but up to 29% lower C capture during dry seasons across the 2000–18 period. In both seasons, the rate of C capture by plantations was less stable across years, and decreased more during drought years (i.e. lower resistance to drought), compared to forests. Thus, even as certain monodominant plantations could match natural forests for C capture and storage potential, plantations are unlikely to match the stability—and hence reliability—of C capture exhibited by forests, particularly in the face of increasing droughts and other climatic perturbations. Promoting natural forest regeneration and/or multi-species native tree plantations instead of plantation monocultures could therefore benefit climate change mitigation efforts, while offering valuable co-benefits for biodiversity conservation and other ecosystem services.

Introduction

Tropical forests harbour over two-thirds of global biodiversity and perform vital ecosystem functions necessary for biodiversity conservation and human well-being (Gardner *et al* 2009, Costanza *et al* 2014).

These forests annually sequester around 2.0 Pg (10^{15} g) of carbon (C) from the atmosphere through photosynthesis, and store over 400 Pg C in vegetation and soil pools, thereby strongly regulating atmospheric CO₂ concentrations and global climate (Pan *et al* 2011). With the majority of tropical forests having

been lost or degraded by anthropogenic activity (Watson *et al* 2018), reforestation has emerged as a leading strategy for conserving biodiversity and mitigating climate change (Griscom *et al* 2017, Lewis *et al* 2019).

Reforestation is promoted by major international agreements and policies such as the Bonn Challenge and Paris Climate Accord, with participating countries committing to increase forest cover by nearly 300 Mha in total by 2030 (United Nations 2015, Lewis *et al* 2019). However, even as tree cover has shown an increasing global trend in recent decades (Song *et al* 2018), this trend conceals critical shifts in tree species composition. Specifically, monoculture or monodominant tree plantations—that are widely misclassified as forests—are expanding, while species-rich natural tropical forests continue to be deforested (Puyravaud *et al* 2010, Payn *et al* 2015, Hua *et al* 2016).

An assessment of international commitments toward climate-focused reforestation has revealed that while over 50% of such commitments are for short-rotation (10–20 years) commercial plantations, certain countries (e.g. India) have also committed significant areas to restoring natural forests (Lewis *et al* 2019). However, ongoing reforestation efforts in India predominantly employ non-commercial monoculture/monodominant tree plantations (Seidler and Bawa 2016, Narain and Maron 2018), comprising substantially lower tree diversity than native forests (e.g. dry-deciduous to wet-evergreen forests in India's Western Ghats region harbour 49 species ha⁻¹, on average (Ramesh *et al* 2010)). According to the Indian Government's CAMPA program, which channels payments from projects responsible for deforestation towards compensatory afforestation efforts, plantations of five or fewer species constitute 53% of the 2 35 000 ha planted for reforestation during 2015–18 (data from <http://egreenwatch.nic.in/>; figure S1, available online at stacks.iop.org/ERL/15/034011/mmedia).

It is well established that species-rich natural forests better support plant and animal biodiversity than monodominant plantations (Gibson *et al* 2011). It is also clear that short-rotation plantations do not directly sequester as much carbon as uncut natural forests (Lewis *et al* 2019). It remains unclear, however, whether and how mature or long-rotation (e.g. > 50 y) monodominant plantations differ from species-rich naturally regenerating forests in C sequestering functions, including magnitude and temporal stability of C capture from the atmosphere via photosynthesis, and long-term C storage.

Biodiversity and ecosystem function (BEF) theory predicts that diversity promotes efficient resource use, and increases the likelihood of functionally high-performing species occurring within communities (Cardinale *et al* 2012). Species-rich tree communities are therefore expected to exhibit higher rates of primary

production or atmospheric C capture, and potentially accumulate larger C stocks over time, than average monocultures (Huang *et al* 2018). However, studies have shown that monocultures of highly productive tree species—such as those commonly used in commercial plantations—could match or exceed C capture rates of more species-rich communities (Bonner *et al* 2013, Huang *et al* 2018). Likewise, monocultures of hardwood timber species could accumulate similar or larger C stocks over time than more diverse communities comprising hardwood and softwood species (Bunker *et al* 2005, Hulvey *et al* 2013). The theory thus suggests that differences in C capture rates and C storage between natural forests and monodominant plantations would vary by plantation species and forest type. This highlights the need for empirical studies making comparisons of C capture and storage between plantation monocultures typically used in reforestation programmes, and natural forests.

A second BEF prediction is that diversity increases temporal stability of ecosystem functions, because larger pools of species are more likely to contain species tolerant to different types of perturbations (Hooper *et al* 2005). The theory suggests that species-rich tree communities would exhibit greater temporal stability of C capture rates that would additionally offer higher resistance (i.e. be affected less by) perturbations such as droughts (Jucker *et al* 2014), than monodominant plantations. However, the prediction that species-rich forests would therefore offer more stable (Hulvey *et al* 2013)—and hence reliable (Naeem 2003)—C capture than monodominant plantations remains untested.

This study examines the above predictions of BEF theory in the context of C capture rates and C storage by species-rich natural forests and monodominant tree plantations. The study is based on a unique natural experiment in India's Western Ghats mountains, where the cessation of timber management activities within newly established wildlife reserves during the mid-late 20th century has resulted in mature monodominant plantations (>40 y old) growing alongside naturally regenerating native tropical forests. First, we compare aboveground C stocks, and rates of photosynthetic C capture over the 2000–18 period [indexed using the satellite-derived Enhanced Vegetation Index (EVI)], across mature monodominant teak (*Tectona grandis*) and Eucalyptus (*Eucalyptus spp.*) plantations, and evergreen and moist-deciduous natural tropical forests. In line with the first BEF theory prediction, we expect no consistent differences in C storage and average rates of C capture between species-rich forests and monodominant plantations. Next, we examine inter-annual variation in rates of C capture, and test the second BEF prediction that species-rich natural forests exhibit greater stability of C capture across years, and are less sensitive to droughts, than monodominant plantations.

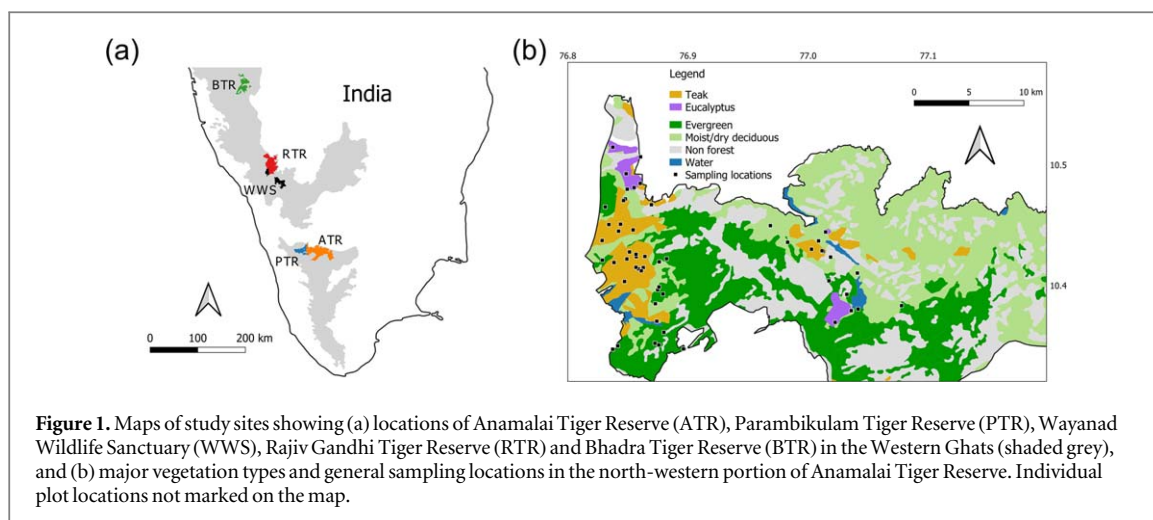


Figure 1. Maps of study sites showing (a) locations of Anamalai Tiger Reserve (ATR), Parambikulam Tiger Reserve (PTR), Wayanad Wildlife Sanctuary (WWS), Rajiv Gandhi Tiger Reserve (RTR) and Bhadra Tiger Reserve (BTR) in the Western Ghats (shaded grey), and (b) major vegetation types and general sampling locations in the north-western portion of Anamalai Tiger Reserve. Individual plot locations not marked on the map.

Table 1. Details of sampling plots in ATR including numbers of plots, mean annual precipitation, mean annual temperature, and average elevation (1 SE in parentheses).

Class	No. of plots	Annual precipitation (mm)	Annual temperature (°C)	Elevation (m)
Evergreen forest	70	1950 (26)	21.8 (0.2)	879 (25)
Deciduous forest	81	1977 (28)	21.8 (0.2)	809 (28)
Teak plantation	64	1850 (24)	22.8 (0.1)	725 (18)
Eucalyptus plantation	27	1752 (21)	22.9 (0.4)	661 (66)

Methods

Study areas

Our study focused on five wildlife reserves in the Western Ghats (8.1–20.1 °N, 73.2–77.6 °E), a 1600 km long mountain chain in peninsular India that forms part of the Western Ghats and Sri Lanka Biodiversity Hotspot (Kumar *et al* 2004). We conducted a field study in the Anamalai Tiger Reserve (ATR), and an analysis of Landsat satellite imagery across ATR, Parambikulam Tiger Reserve (PTR), Rajiv Gandhi Tiger Reserve (RTR), Wayanad Wildlife Sanctuary (WWS), and Bhadra Tiger Reserve (BTR) (figure 1(a)).

The study areas were important centres for forestry operations from the colonial period (1800s), and were exploited for timber and for raising plantations of commercially important species such as teak and Eucalyptus spp. in place of native evergreen and moist-deciduous forests (Chandran 1997, Sekar and Ganesan 2003). Strengthening of Indian conservation laws including designation of wildlife reserves during 1950–80 shifted management priorities from forestry toward conservation in these reserves. Presently, these reserves support significant areas (6%–32%) under mature, monodominant teak and Eucalyptus stands—the former being more extensive—raised as plantations before 1980, but not harvested due to the cessation of forestry operations (information from official management plans for the individual reserves). Alongside these plantations grow mixed-species native wet-evergreen and moist-deciduous tropical forests (Pascal 1986) that were selectively logged before 1980, but

have since largely been freed from extractive or commercial use.

Our study system thus provides an opportunity for comparing the C sequestering functions of monodominant plantations raised for reforestation/afforestation or long-rotation harvest, and species-rich natural forests that may be secured by averting deforestation, or that could emerge over time through reforestation via natural succession or active restoration. Although not exactly matched for age (some natural forests may be older than plantations), our system nevertheless offers a unique, long-term perspective on the roles of these contrasting types of forests in fighting climate change.

Forest inventory plots

We conducted a field study in ATR to assess forest structure, species richness and aboveground C storage by trees in two natural forest types—evergreen forests (EF), moist-deciduous forests (DF)—and in two monodominant plantation types—teak plantations (TP) and Eucalyptus (mainly, *E. tereticornis* and *E. grandis*) plantations (EP). A total of 242 square plots of 20 m (0.04 ha) side was sampled across the four habitats, including 70, 81, 64 and 27 plots in EF, DF, TP and EP, respectively (figure 1(B); table 1). All plots lay within a c. 600 km² region that is relatively homogeneous in terms of elevation, rainfall and temperature (table 1). Soils in the study area are classified as Alfisols of a red, sandy sub-type (source: National Atlas and Thematic Mapping Organization *via* India Biodiversity portal).

Plots were sampled by one of the authors (AG) and field assistants during September 2018–June 2019. We recorded species identity, girth at breast height (1.3 m; gbh, in cm) using a tape measure, and tree height (in m, using Nikon Monarch 7i VR laser range finder) of all trees ≥ 30 cm gbh (9.5 cm diameter at breast height–dbh) in each plot. Species were identified in the field (data collectors have 4–20 years' experience conducting botanical surveys in the area), and from collected specimens with aid of floral keys (Gamble and Fischer 1935, Pascal and Ramesh 1997, Neginhal 2004, Ganesan *et al* 2012, Krishen 2014, Page 2017).

Aboveground C storage

Aboveground biomass (AGB_{est} , kg) of individual trees was estimated using a general allometric equation from Chave *et al* (2014):

$$AGB_{est} = 0.0673 \times (\rho D^2 H)^{0.976},$$

where ρ is wood density (g cm^{-3}), D is tree diameter at breast height (cm), and H is tree height (m). Species' wood densities were obtained from published sources (Zanne *et al* 2009, Osuri *et al* 2014). Trees belonging to species that lacked published wood density estimates (10% of all individuals) were assigned the community-weighted average wood density of their respective plots. The carbon fraction of aboveground biomass was assumed as 47% (Thomas and Martin 2012). Plot-level estimates for aboveground C storage ($\text{Mg } 0.04 \text{ ha}^{-1}$) were obtained by totalling C stocks across all trees within each plot.

Locations for satellite data analysis

Two sets of ground locations were used in analyses of Landsat satellite data. The first set, corresponding to the 242 sample plots in ATR, was created by placing circular buffers of 30 m radius around the centroids of each plot. The purpose of creating buffers was to sample the immediate neighbourhood of 30 m pixels (nine) surrounding each location.

The second dataset comprised pairs of natural forest and plantation locations from across ATR, PTR, WWS, RTR and BTR. We used a vegetation map of the Western Ghats comprising 14 classes (Renard *et al* 2010) to identify edges between teak/Eucalyptus plantations and evergreen/moist-deciduous forests within each reserve. At a randomly selected location along the length of each edge, we placed two 30 m radius circles in forests and plantations at a perpendicular distance of 200 m on either side. We ground-truthed the locations and repositioned our samples—if needed—based on site visits (April–May 2018), visual inspection of high-resolution imagery on the Google Earth platform, and consultations with local experts. This exercise produced a set of 48 forest-plantation pairs, including 32 and eight pairs of deciduous forest with teak and Eucalyptus plantations, respectively, and eight evergreen forest-teak plantation pairs across the five reserves.

Rates of C capture

The Enhanced Vegetation Index (EVI) is an index of photosynthetically active vegetation derived from remotely sensed reflectance in near-infrared (NIR), red (R) and blue (B) wavelengths (Huete *et al* 2002). This index is known to correlate positively with field-based estimates of gross primary production (GPP), or C capture via photosynthesis (Rahman *et al* 2005, Huete *et al* 2006, Glenn *et al* 2008, Huete *et al* 2008).

We calculated EVI of all cloud-free ($\leq 10\%$ cloud cover) scenes spanning the ATR plots from January 2000 to April 2019 using the surface reflectance products of the USGS Landsat-7 and Landsat-8 platforms (USGS 2017).

$$EVI = 2.5 \times \frac{(NIR - R)}{(NIR + 6 \times R - 7.5 \times B + 1)}.$$

Cloud- and shade-covered pixels, and no-data (Landsat-7 SLC-off) pixels were excluded from subsequent analysis.

Next, taking into consideration the timing of the Indian summer monsoon (June–September) which is the main source of rainfall in the Western Ghats, we calculated median EVIs across all scenes within the post-monsoon wet season (September–December), and within the subsequent dry season (January–April), for each year. Many deciduous species in the region, including teak, shed and regrow leaves over the latter period. Estimates of annual post-wet and dry season median EVIs were based on a median of 1 scene per year (range: 0–3) for post-wet seasons and a median of 3 scenes per year (range: 0–6) for dry seasons. Finally, we extracted year-wise post-wet and dry season median EVIs for the 242 forest plots in ATR and the 96 locations (48 forest-plantation pairs) across the five focal wildlife reserves, by averaging over pixels contained within individual 30 m buffers. See figure S2 for a flowchart of EVI data processing and analysis steps.

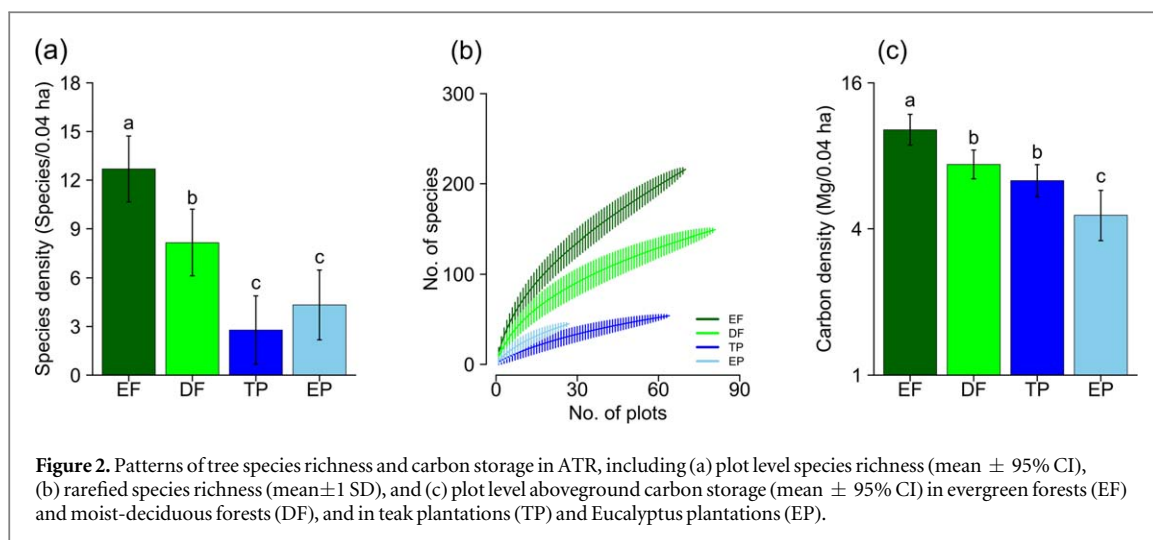
Analysis

Tree species richness and aboveground carbon storage

We used (generalized) linear models with forest/plantation type as the predictor variable to test for differences in number of tree species per plot (species density; Poisson model) and C storage per plot (carbon density; log-transformed response + Gaussian model) between evergreen and deciduous forests, and teak and Eucalyptus plantations across the 242 ATR plots. We also examined treatment-level differences in tree species richness across the four habitats using a plot-based rarefaction.

Average rates and stability of C capture

Average rates of C capture during dry-seasons and wet-seasons were estimated as the average of year-wise seasonal median EVIs over the 2000–18 period at each plot location. Stability of C capture was estimated as the reciprocal of the coefficient of variation of year-wise dry- and wet-season median EVIs for each



location over the same period. We used linear (Gaussian) models to test for differences in average and stability of C capture rates between the four habitat types. Separate models were run for wet and dry seasons.

Next, we explored the influence of climatic variability on C capture stability by assessing differences in average EVI between drought years and all (drought/non-drought) years for the four forest/plantation types in ATR. We identified drought years based on the long-term (1988–2018) average and standard deviation of annual precipitation at each plot, based on the CHIRPS dataset (<https://chc.ucsb.edu/data/chirps/>), and on the regional Standardized Precipitation Index (SPI) of drought (Aadhar and Mishra 2017). We classified drought years as those with annual rainfall one or more standard deviations lower than the long-term average (figure S3), and with SPI index values lower than -1.2 ('severe drought': Aadhar and Mishra (2017)). By this approach, 2002, 2003, 2013 and 2016 were identified as drought years in ATR over the 2000–18 period.

We calculated an EVI difference metric EVI_{diff} as the log-transformed ratio of average EVIs across drought years (2002, 03, 13, 16) to the overall average EVI. Increasingly negative values of EVI_{diff} correspond to greater declines of C capture during drought years relative to the overall average. We used a linear model to compare EVI_{diff} across the four forest/plantation types.

Multi-site analysis

Finally, to explore the wider relevance of patterns observed in ATR, we conducted a multi-site analysis of C capture rates and stability in natural forests and plantation forests across five wildlife reserves in the Western Ghats (ATR, PTR, RTR, BTR and WWS). We assessed average EVI and stability of EVI over 2000–18 for the 96 locations that constituted the 48 forest-plantation spatial pairs within these reserves, separately for wet and dry seasons. For each pair, we

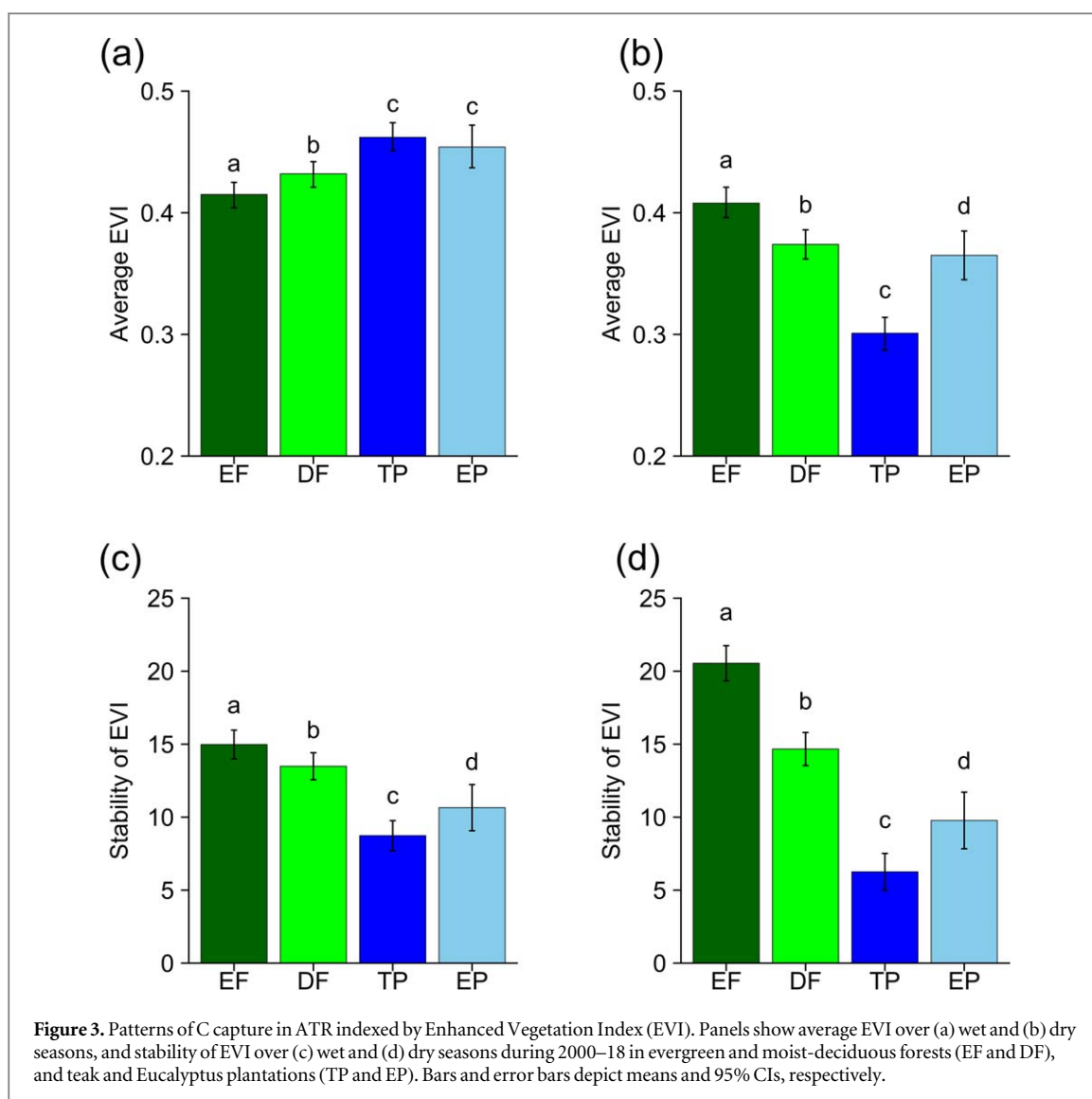
calculated the log-response ratio of average EVI in plantation to forest (LRR_{av}), and the log-response ratio of stability of EVI in plantation to forest (LRR_{st}). We estimated means and 95% confidence intervals (95% CIs) of LRR_{av} and LRR_{st} across plantation (TP or EP) and forest (EF or DF) pairs during wet and dry seasons, and interpreted non-overlap of 95% CIs of the LRRs with zero as indicative of consistent differences between plantations and forests.

All data processing and analyses were performed in the R statistical and programming environment (R Core Team 2018) and the Google Earth Engine platform (Gorelick *et al* 2017).

Results

Tree species richness and aboveground carbon storage

In the Anamalai Tiger Reserve (ATR), teak and Eucalyptus plantations had fewer tree species (3 and 6 species on average, respectively) than natural evergreen and deciduous forests (14 and 9 species, respectively) at the plot level (species density: figure 2(a)), and cumulatively fewer species across plots (rarefied species richness: figure 2(b)). Aboveground C storage per plot (carbon density) was highest in evergreen forest ($12.2 \text{ Mg } 0.04 \text{ ha}^{-1}$, on average), followed by deciduous forest ($9.6 \text{ Mg } 0.04 \text{ ha}^{-1}$) and teak plantation ($7.0 \text{ Mg } 0.04 \text{ ha}^{-1}$) with statistically similar (average of each group lies within the 95% CIs range of the other) C stocks, while Eucalyptus plantations had the lowest carbon density ($5.5 \text{ Mg } 0.04 \text{ ha}^{-1}$) of the four forest types (figure 2(c)). To test for potential biases arising from variation in mean annual precipitation (MAP) across the four forest types, we re-ran our models with MAP included as an additional predictor. Including MAP as a predictor did not alter model predictions (table S1), suggesting that differences in species and carbon density across forest/plantation types are not simply an artefact of differences in MAP.



Average rates and stability of C capture

Wet-season C capture rates were 4%–9% higher in teak and Eucalyptus plantations (average EVI: 0.46 and 0.45, on average, respectively) than in evergreen and deciduous forests (average EVI: 0.42 and 0.44, respectively), but dry-season average EVIs of teak and Eucalyptus plantations (0.30 and 0.36, respectively) were 3%–29% lower than those of evergreen and deciduous forests (0.42 and 0.37, respectively) (figures 3(a), (b)). By contrast, temporal stability of C capture in forests—especially evergreen—was consistently higher than plantations over wet and dry seasons (figures 3(c), (d)). The differences in average and stability of C capture across forests and plantations were evident even after accounting for variation explained by MAP (table S1). Moreover, excluding areas that experienced fire during a given year (source: Modis Terra Thermal Anomalies & Fire data accessed via the Earth Engine platform) from the analysis did not alter the results, indicating that our results are not biased by variation in fire occurrence (table S1).

C capture by plantations appeared less resistant (i.e. decreased more) to drought than that of natural forests. Wet season EVIs of forests during drought years differed less from their corresponding overall averages ($EVI_{diff} = 0.00 - -0.03$; 0%–3% decrease) compared to plantations (5%–8% decrease) (figures 4(a); S4). Differences between the responses of forests and plantations to drought were even more pronounced among dry season EVIs (forests: 2%–6% declines; plantations 12%–14% declines) (figures 4(b); S4), and were not biased by variation in MAP or fire (table S1).

Additionally, for teak plantations in ATR, we explored relationships of C storage and average and stability of C capture with approximate plantation ages (table S2) using pairwise correlations (all Eucalyptus plantations being of similar age, were not included). Teak plantation age correlated positively with aboveground C stocks, negatively with average EVI (dry season), stability of EVI, and EVI_{diff} (i.e. greater declines of EVI during drought years (relative to long-term average) among older plantations; table 2).

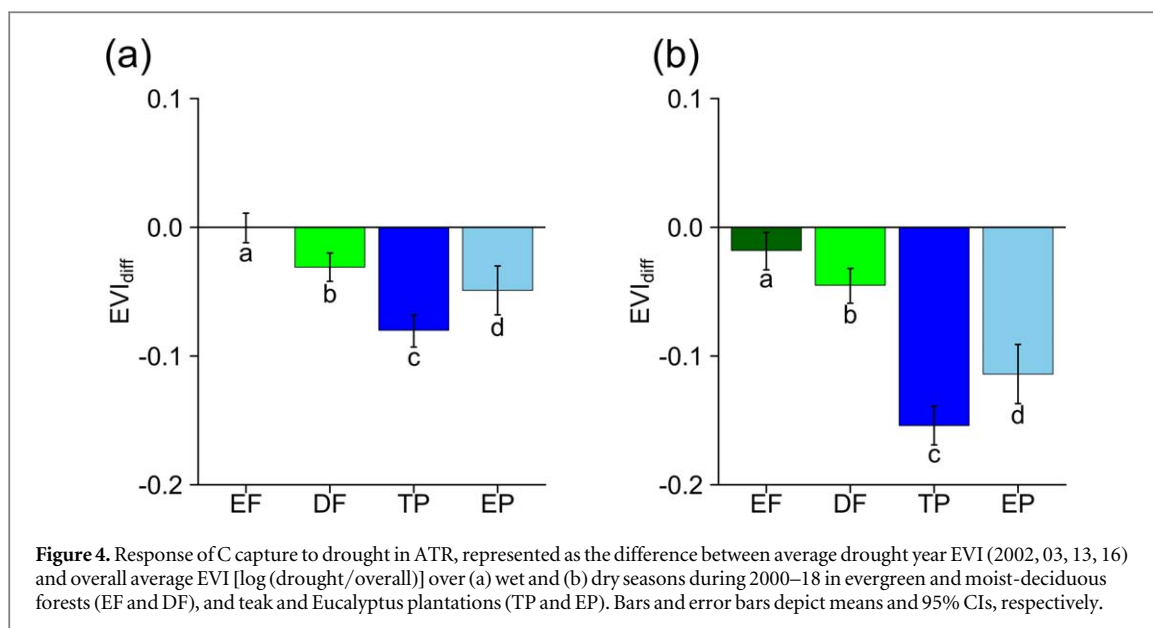


Table 2. Pearson’s correlation coefficients between the age of teak plantations and the different indicators of C sequestration in the Anamalai Tiger Reserve. Correlations with 95% confidence interval estimates not overlapping zero are marked with *.

Indicator	Correlation with plantation age
Aboveground carbon stocks	0.44*
Average EVI (Wet season)	0.01
Average EVI (Dry season)	−0.33*
Stability of EVI (Wet season)	−0.37*
Stability of EVI (Dry season)	−0.39*
EVI _{diff} (Wet season)	−0.25*
EVI _{diff} (Dry season)	−0.64*

Multi-site analysis

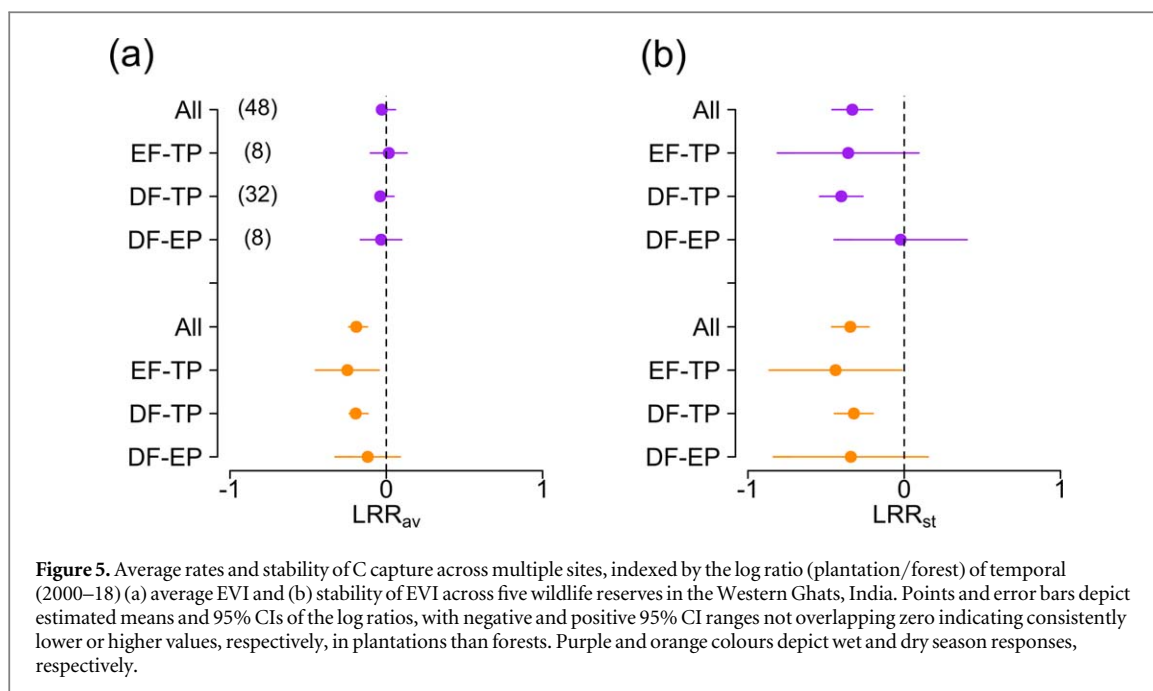
Patterns of C capture in evergreen and deciduous forests, and teak and Eucalyptus plantations across multiple locations in the Western Ghats generally matched those observed in ATR. The average EVI of forests and plantations did not differ consistently during the wet season (95% CI range of LRR_{av} includes zero), but plantations had consistently lower EVI than forests during dry seasons (negative 95% CI range of LRR_{av} ; figure 5(a)). These patterns were driven by the DF-TP contrast, which constituted 67% of all edge pairings, while EF-TP and DF-EP showed qualitatively similar responses, but were associated with wider uncertainty estimates (figure 5). Forests showed greater temporal stability of EVI than plantations, on average, in both wet and dry seasons, but with 95% CIs overlapping zero for EF-TP and DF-EP comparisons, possibly due to the limited sample sizes of these types of pairs (figure 5(b)).

Discussion

With forest plantations and natural forest regeneration gaining global significance as strategies for mitigating

climate change, understanding the long term carbon storage potential of different types of reforestation strategies, and how effectively and reliably they capture carbon from the atmosphere, is critical for reforestation policy and practice. Our study in India’s Western Ghats compared multiple facets of C sequestration across mature monodominant plantations and species-rich natural tropical forests. Our findings reveal interesting contrasts across indicators of C sequestration quantity and stability in plantations and natural forests.

On one hand, indicators related to quantity, namely aboveground C stocks and rates of photosynthetic C capture (average EVI), did not differ consistently between species-rich natural forests and species-poor plantations in our study. Hardwood teak plantations had similar C stocks as moist-deciduous forests (but substantially lower C stocks than evergreen forests), while fast-growing Eucalyptus plantations had comparatively low C stocks, but similar to greater rates of C capture than both forest types across wet and dry seasons. While these patterns might partly be due to differences in age—i.e. relatively younger plantations store less C but exhibit higher rates of C capture—they nevertheless support the BEF theory prediction that monocultures of certain species could match or surpass species-rich forests for C storage or average rates of C capture (Bonner *et al* 2013, Hulvey *et al* 2013, Huang *et al* 2018). While our study focused on mature, unharvested plantations, harvesting plantations for manufacture of long-lived wood products could effectively increase C capture and storage (Keith *et al* 2014). However, the climate regulating benefits of the latter approach remain questionable, because harvesting of timber is also likely to release significant amounts of CO₂ to the atmosphere (Keith *et al* 2014, Lewis *et al* 2019).



In contrast to C storage and average rates of C capture, and in agreement with BEF theory (Yachi and Loreau 1999, Hooper *et al* 2005), the stability of C capture rates was consistently higher in species-rich forests (EF > DF) than in monodominant plantations (EP > TP) in our study. Furthermore, our findings indicate that this difference in stability is likely due to plantations showing lower resistance of C capture to drought compared to forests. Moreover, variation with age across teak plantations suggest that these differences in C capture stability are likely to persist, and possibly increase, over time. Collectively, these results suggest that species-rich natural forests may be more reliable than plantations as agents for terrestrial C sequestration (Naeem 2003), especially given ongoing and predicted increases in climatic perturbations such as droughts in south Asia (Singh *et al* 2014) and several other regions globally (Dai 2012).

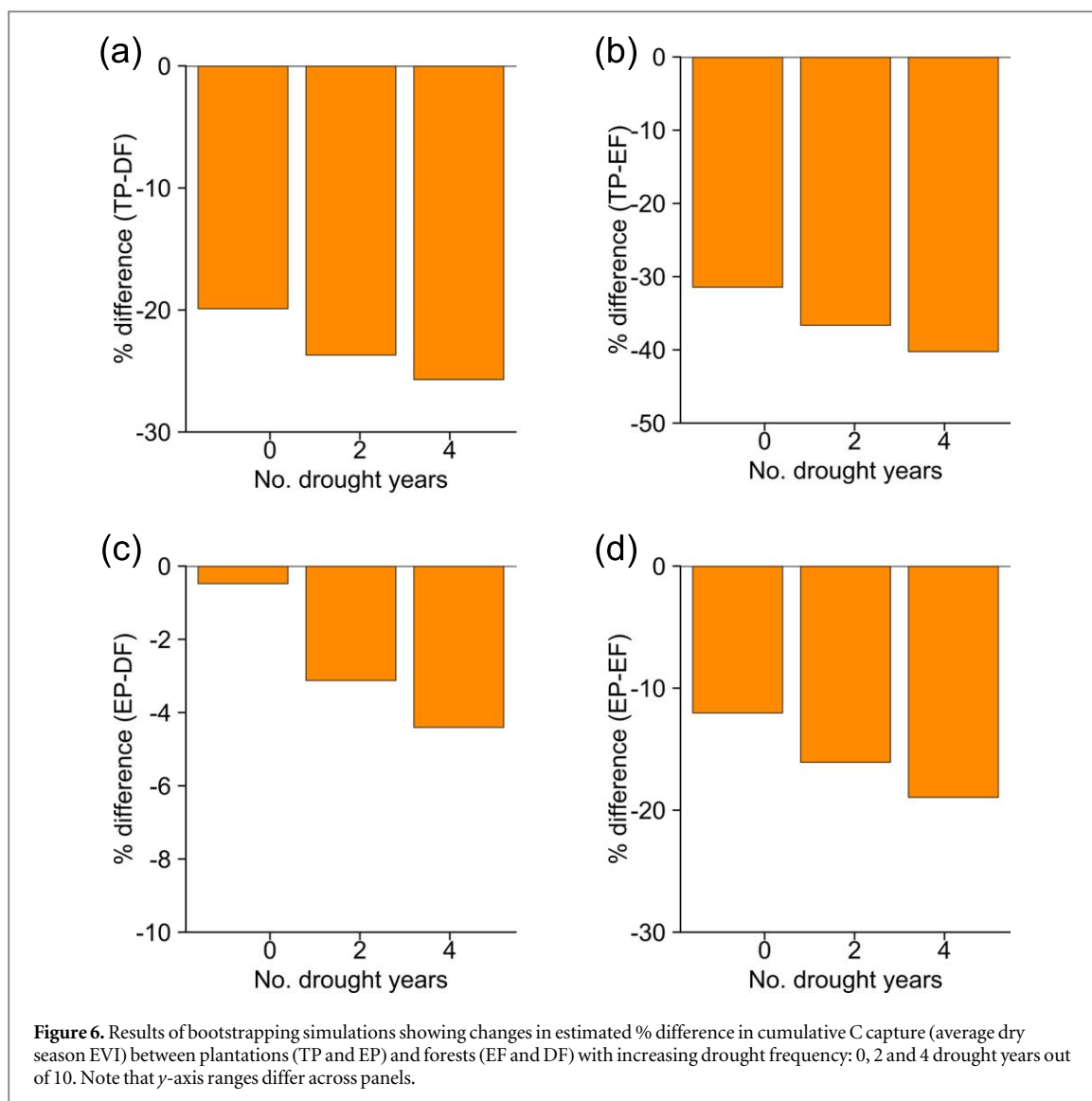
We illustrate the above argument with a simple bootstrapping simulation. In ATR, the difference in cumulative C capture (i.e. cumulative average EVI) between teak plantations and deciduous forests across 10 randomly selected dry seasons (sampled with replacement; 100 iterations) increased from 21% lower in teak plantations on average when considering non-drought years alone, to 23% and 27% lower in teak plantations when two and four drought years, respectively, were included in the random samples (figure 6(a)). Similar patterns were observed among other forest-plantation contrasts across dry seasons (figures 6(b)–(d)), and to a lesser extent across wet seasons (figure S5) in our simulations.

We focused on trees in this study because of their dominant influence on the C cycles of mature forest and plantation ecosystems (Lü *et al* 2010, Chen *et al* 2015). Forest/plantation C cycles also comprise

several other pools (e.g. coarse woody debris) and fluxes (e.g. soil respiration) (Malhi 2012), but how these differ between forests and plantations, and ultimately shape C capture, storage and release to the atmosphere by these ecosystems, remains poorly studied. Further research assessing these other C pools and fluxes can shed light on how patterns of photosynthetic C capture and storage observed at the level of tree communities translate in terms of overall C sequestration at the ecosystem scale in species-rich natural forests and monodominant plantations.

Conclusion

A strict focus on quantity (potential C capture rates and storage) might suggest equivalence of monoculture/monodominant plantations and high-diversity forests for mitigating climate change (Bonner *et al* 2013, Hulvey *et al* 2013). However, our findings suggest that when assessed for both quantity and quality, in terms of reliability of C capture in the face of perturbation such as droughts, forests are superior to, and irreplaceable by, plantations as agents of terrestrial C sequestration. This is consistent with findings from other biomes such as grasslands, which too might be more reliable than plantations for sequestering carbon, and which are facing a significant threat from ongoing and planned expansions of plantations (Bond *et al* 2019). Policies that facilitate land transitions from natural forests (and other ecosystems) to plantations—e.g. India's compensatory afforestation programme—can therefore have lasting detrimental impacts on terrestrial carbon sequestration, in addition to posing a significant threat to biodiversity (Narain and Maron 2018). Our findings thus underscore the need for policy changes



that increase focus on protecting and restoring natural forests and/or mixed plantations of native tree species—instead of promoting low-diversity plantations (Lewis *et al* 2019)—as a more appropriate strategy for sequestering carbon in an increasingly variable and drought-prone climate. Apart from likely benefits for climate change mitigation, such policy changes would also generate valuable co-benefits for biodiversity conservation and other ecosystem services.

Acknowledgments

We are grateful to Rajesh, Sathish, Sundar Raj and Moorthy for assistance during fieldwork. We thank Divya Mudappa, Raman Kumar, M D Madhusudan, Girish D V, Chengappa S K, Srinivasan Kasinathan and Sreedhar Vijaykrishnan for sharing expertise and technical inputs. We thank the Tamil Nadu Forest Department for research permits, and appreciate guidance from V Ganesan (IFS), S Thangaraj Panneerselvam. AMO received a fellowship and research

funding from the NatureNet Science Fellows Program and the Earth Institute Fellows Program. TRSR acknowledges funding and partnership from Rohini Nilekani Philanthropies, Arvind Datar, and the AMM Murugappa Chettiar Research Centre for long-term rainforest restoration and recovery research in the Anamalais.

Data availability statement

The data that support the findings of this study are openly available at <https://doi.org/10.25412/iop.11324132.v1>.

ORCID iDs

Anand M Osuri  <https://orcid.org/0000-0001-9909-5633>

Abhishek Gopal  <https://orcid.org/0000-0002-3020-4122>

T R Shankar Raman  <https://orcid.org/0000-0002-1347-3953>

Ruth DeFries  <https://orcid.org/0000-0002-3332-4621>

Susan C Cook-Patton  <https://orcid.org/0000-0002-7194-4397>

Shahid Naeem  <https://orcid.org/0000-0002-6569-2648>

References

- Aadhar S and Mishra V 2017 High-resolution near real-time drought monitoring in South Asia *Sci. Data* **4** 170145
- Bond W J, Stevens N, Midgley G F and Lehmann C E R 2019 The trouble with trees: afforestation plans for Africa *Trends Ecol. Evol.* **34** 963–5
- Bonner M T L, Schmidt S and Shoo L P 2013 A meta-analytical global comparison of aboveground biomass accumulation between tropical secondary forests and monoculture plantations *Forest Ecol. Manage.* **291** 73–86
- Bunker D E, DeClerck F, Bradford J C, Colwell R K, Perfecto I, Phillips O L, Sankaran M and Naeem S 2005 Species loss and aboveground carbon storage in a tropical forest *Science* **310** 1029–31
- Cardinale B J *et al* 2012 Biodiversity loss and its impact on humanity *Nature* **486** 59–67
- Chandran M S 1997 On the ecological history of the Western Ghats *Curr. Sci.* **73** 146–55
- Chave J *et al* 2014 Improved allometric models to estimate the aboveground biomass of tropical trees *Glob. Change Biol.* **20** 3177–90
- Chen Y, Liu Z, Rao X, Wang X, Liang C, Lin Y, Zhou L, Cai X-A and Fu S 2015 Carbon storage and allocation pattern in plant biomass among different forest plantation stands in Guangdong, China *Forests* **6** 794–808
- Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson S J, Kubiszewski I, Farber S and Turner R K 2014 Changes in the global value of ecosystem services *Glob. Environ. Change* **26** 152–8
- Dai A 2012 Increasing drought under global warming in observations and models *Nat. Clim. Change* **3** 52–8
- Gamble J and Fischer C 1935 *Flora of the Presidency of Madras. Parts I to XI*, vol 1-3 (London: Secretary of State for India)
- Ganesan R, Kavitha A, Deepthi N and Gladwin Joseph S C 2012 *Common Dryland Trees of Karnataka: Bilingual Field Guide* (Bengaluru, India: Ashoka Trust for Research in Ecology and the Environment)
- Gardner T A, Barlow J, Chazdon R, Ewers R M, Harvey C A, Peres C A and Sodhi N S 2009 Prospects for tropical forest biodiversity in a human-modified world *Ecol. Lett.* **12** 561–82
- Gibson L *et al* 2011 Primary forests are irreplaceable for sustaining tropical biodiversity *Nature* **478** 378–81
- Glenn E P, Huete A R, Nagler P L and Nelson S G 2008 Relationship between remotely-sensed vegetation indices, canopy attributes and plant physiological processes: What vegetation indices can and cannot tell us about the landscape *Sensors* **8** 2136–60
- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R 2017 Google Earth Engine: Planetary-scale geospatial analysis for everyone *Remote Sens. Environ.* **202** 18–27
- Griscom B W *et al* 2017 Natural climate solutions *Proc. Natl Acad. Sci. USA* **114** 11645–50
- Hooper D U *et al* 2005 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge *Ecol. Monogr.* **75** 3–35
- Hua F, Wang X, Zheng X, Fisher B, Wang L, Zhu J, Tang Y, Yu D W and Wilcove D S 2016 Opportunities for biodiversity gains under the world's largest reforestation programme *Nat. Commun.* **7** 12717
- Huang Y *et al* 2018 Impacts of species richness on productivity in a large-scale subtropical forest experiment *Science* **362** 80–3
- Huete A R, Didan K, Miura T, Rodriguez E P, Gao X and Ferreira L G 2002 Overview of the radiometric and biophysical performance of the MODIS vegetation indices *Remote Sens. Environ.* **83** 195–213
- Huete A R, Didan K, Shimabukuro Y E, Ratana P, Saleska S R, Huttyra L R, Yang W, Nemani R R and Myneni R 2006 Amazon rainforests green-up with sunlight in dry season *Geophys. Res. Lett.* **33** L06405
- Huete A R, Restrepo-Coupe N, Ratana P, Didan K, Saleska S R, Ichii K, Panuthai S and Gamo M 2008 Multiple site tower flux and remote sensing comparisons of tropical forest dynamics in Monsoon Asia *Agric. Forest Meteorol.* **148** 748–60
- Hulvey K B, Hobbs R J, Standish R J, Lindenmayer D B, Lach L and Perring M P 2013 Benefits of tree mixes in carbon plantings *Nat. Clim. Change* **3** 869–74
- Jucker T, Bouriaud O, Avacaritei D and Coomes D A 2014 Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes *Ecol. Lett.* **17** 1560–9
- Keith H, Lindenmayer D, Mackey B, Blair D, Carter L, McBurney L, Okada S and Konishi-Nagano T 2014 Managing temperate forests for carbon storage: impacts of logging versus forest protection on carbon stocks *Ecosphere* **5** 75
- Krishen P 2014 *Jungle Trees of Central India: A Field Guide for Tree Spotters* (India: Penguin)
- Kumar A, Pethiyagoda R and Mudappa D 2004 *Hotspots Revisited—Earth's Biologically Richest and Most Endangered Ecoregions. CEMEX, Mexico* (Mexico: CEMEX) pp 152–7
- Lewis S L, Wheeler C E, Mitchard E T and Koch A 2019 Restoring natural forests is the best way to remove atmospheric carbon *Nature* **568** 25–8
- Lü X-T, Yin J-X, Jepsen M R and Tang J-W 2010 Ecosystem carbon storage and partitioning in a tropical seasonal forest in Southwestern China *Forest Ecol. Manage.* **260** 1798–803
- Malhi Y 2012 The productivity, metabolism and carbon cycle of tropical forest vegetation *J. Ecol.* **100** 65–75
- Naeem S 2003 *The importance of Species: Perspectives on Expendability and Triage* ed P Kareiva and S A Levin (Princeton: Princeton University Press) pp 109–39
- Narain D and Maron M 2018 Cost shifting and other perverse incentives in biodiversity offsetting in India *Conserv. Biol.* **32** 782–8
- Neginhal S G 2004 *Forest Trees of South India* (Bengaluru, India: S G Neginhal)
- Osuri A M, Kumar V S and Sankaran M 2014 Altered stand structure and tree allometry reduce carbon storage in evergreen forest fragments in India's Western Ghats *Forest Ecol. Manage.* **329** 375–83
- Page N 2017 *Endemic Woody Plants of the Western Ghats* (Bengaluru, India: Rufford Small Grants Foundation)
- Pan Y *et al* 2011 A large and persistent carbon sink in the world's forests *Science* **333** 988–93
- Pascal J-P and Ramesh B-R 1997 *Field Key to the Trees and Lianas of the Evergreen Forests of the Western Ghats, India* (Pondicherry: Institut Français De Pondichéry)
- Pascal J 1986 *Explanatory Booklet on the Forest Maps of South India* (Pondicherry: Institut Français De Pondichéry)
- Payn T, Carnus J-M, Freer-Smith P, Kimberley M, Kollert W, Liu S, Orazio C, Rodriguez L, Silva L N and Wingfield M J 2015 Changes in planted forests and future global implications *Forest Ecol. Manage.* **352** 57–67
- Puyravaud J-P, Davidar P and Laurance W F 2010 Cryptic destruction of India's native forests *Conserv. Lett.* **3** 390–4
- Rahman A F, Sims D A, Cordova V D and El-Masri B Z 2005 Potential of MODIS EVI and surface temperature for directly estimating per-pixel ecosystem C fluxes *Geophys. Res. Lett.* **32** L19404
- Ramesh B R, Venugopal P D, Pélissier R, Patil S V, Swaminath M H and Coutron P 2010 Mesoscale patterns in the floristic composition of forests in the central Western Ghats of Karnataka, India *Biotropica* **42** 435–43
- Renard Q, Ramesh B R, Muthusankar G and Pelissier R 2010 Data Paper—High resolution vegetation cover data for the Southern

- Western Ghats of India *Pondy Papers in Ecology* (Pondicherry: Institut Français de Pondichéry)
- R Core Team 2018 R: A language and environment for statistical computing *R Foundation for Statistical Computing* (Austria: Vienna)
- Seidler R and Bawa K S 2016 India faces a long and winding path to green climate solutions *Proc. Natl Acad. Sci. USA* **113** 12337–40
- Sekar T and Ganesan V 2003 *Forest History of Anamalais, Tamil Nadu* (Chennai, India: Tamil Nadu, Tamil Nadu Forest Department)
- Singh D, Tsiang M, Rajaratnam B and Diffenbaugh N S 2014 Observed changes in extreme wet and dry spells during the South Asian summer monsoon season *Nat. Clim. Change* **4** 456
- Song X-P, Hansen M C, Stehman S V, Potapov P V, Tyukavina A, Vermote E F and Townshend J R 2018 Global land change from 1982 to 2016 *Nature* **560** 639–43
- Thomas S C and Martin A R 2012 Carbon content of tree tissues: a synthesis *Forests* **3** 332–52
- United Nations 2015 *Paris Agreement* (Paris: United Nations)
- USGS 2017 Product guide: Landsat Surface Reflectance-derived spectral indices Version 3.6. (<https://usgs.gov/land-resources/nli/landsat/landsat-surface-reflectance-derived-spectral-indices>)
- Watson J E M *et al* 2018 The exceptional value of intact forest ecosystems *Nat. Ecol. Evol.* **2** 599–610
- Yachi S and Loreau M 1999 Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis *Proc. Natl Acad. Sci. USA* **96** 1463–8
- Zanne A E, Lopez-Gonzalez G, Coomes D A, Ilic J, Jansen S, Lewis S L, Miller R B, Swenson N G, Wiemann M C and Chave J 2009 Data from: towards a worldwide wood economics spectrum. Dryad Digital Repository (<https://doi.org/10.5061/dryad.234>)