Title: Tree species diversity drives the land surface phenology of seasonally dry tropical woodlands

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Author contribution statement

JLG conceived the study, conducted the analysis, and wrote the first draft of the manuscript. AS coordinated field data collection in Zambia. All authors contributed to manuscript revisions.

Data accessibility statement

Field data used in this study are from the Zambian Integrated Land Use Assessment (ILUA-II). Data were cleaned and archived by the SEOSAW project (The Socio-Ecological Observatory for Studying African Woodlands). An anonymised version of the field data are available at the following DOI: `https://doi.org/10.7488/ds/7735`. Code developed for data analysis can be found here: `https://github.com/johngodlee/zambia_phenology`.

Abstract

1. Seasonal foliage display (leaf phenology) is a key determinant of ecosystem function. Variation in land surface phenology, observed via space-borne remote sensing, can be explained at broad spatial scales by climate, but we lack understanding of how vegetation structure and floristic diversity mediates these relationships. This lack of understanding hampers our ability to predict changes in phenology and therefore ecosystem function, in light of rapid ongoing shifts in biodiversity and ecosystem structure due to land use and climate change.

2. We combined a network of 619 vegetation monitoring sites across seasonally dry tropical deciduous woodlands in Zambia with land surface phenology metrics to investigate the role of tree species diversity, composition and vegetation structure on patterns of land surface phenology, including the phenomenon of pre-rain green-up.

3. Tree species diversity was associated with earlier pre-rain green-up, a longer growing season, and greater cumulative foliage production. Independent of diversity, proportional abundance of Detarioideae species (subfamily of Fabaceae) was associated with a longer growing season by facilitating earlier pre-rain green-up. Woodland stands with larger trees green up earlier, suggesting access to deep groundwater reserves. Senescence metrics showed variation among sites, but were not well explained by precipitation, temperature, structure or diversity.

4. **Synthesis:** Tree diversity, composition and structure are co-determinants of seasonal patterns of foliage display in seasonally dry tropical deciduous woodlands, as measured via land surface phenology, at regional scale. Our study identifies both a niche complementarity effect whereby diverse woodlands exhibit longer growing seasons, as well as a mass-ratio effect whereby detarioid species drive earlier pre-rain green-up, providing insights into the mechanisms underlying the biodiversity ecosystem function relationship in this biome. We stress the importance of considering biotic controls on ecosystem functioning in the next generation of earth-system models predicting the response of communities to global change.

1 Introduction

Foliage forms the primary interface between the vegetated land surface, the atmosphere and incoming solar radiation (Gu et al., 2003; Penuelas et al., 2009). Seasonal cycles of foliage production (leaf phenology) play an important role in regulating global carbon, water and nitrogen cycles (Garonna et al., 2016). Vegetation indices derived from remote sensing data, used as a proxy for foliage display (land surface phenology), have been used to constrain estimates of primary productivity in terrestrial biosphere models (Bloom et al., 2016; Helman, 2018), and to characterise the functional response of vegetation to various climate drivers (Richardson et al., 2013). Previous studies have identified environmental drivers of land surface phenology (Adole et al., 2019; Guan et al., 2014), but we lack understanding of how the floristic diversity and structure of the vegetation itself mediates these relationships (Whitley et al., 2017; Pau et al., 2011).

At continental scale, patterns of land surface phenology can be explained adequately using only climatic factors, namely precipitation, diurnal temperature oscillation, and photoperiod (Adole et al., 2018b; Adole et al., 2019; Guan et al., 2014), but significant local variation exists within biomes in the timing of foliage display that cannot be attributed solely to abiotic environment (Stöckli et al., 2011). Additionally, we lack a mechanistic understanding of the biotic controls on land surface phenology, which hampers our ability to make informed predictions of change in phenology under global environmental change. It has been repeatedly suggested that the diversity, composition, and structure of plant communities plays a role in determining ecosystem response to abiotic cues driving patterns of land surface phenology (Adole et al., 2018a; Jeganathan et al., 2014; Fuller, 1999), owing to differences in phenological strategy among species, but studies on this are lacking (Ma et al., 2022). Indeed, ground observations find wide variation in temporal patterns of foliage display among plant communities within a given biome (Seyednasrollah et al., 2019), but this variation is rarely represented in predictive models of biosphere-atmosphere exchanges (Scheiter et al., 2013; Pavlick et al., 2013).

Across the miombo woodlands of southern Africa, the largest woodland formation in the region (White, 1983), seasonal oscillations in water availability drive strong seasonal cycles of foliage display (Chidumayo, 2001; Dahlin et al., 2016). Within miombo woodlands, the phenomenon of pre-rain green-up, where trees produce leaves in advance of seasonal rains, serves as a striking example of phenological response to seasonal rainfall patterns. While pre-rain green-up requires heavy investment in hydraulic architecture to access deep groundwater and to produce embolism resistant hydraulic systems, it may provide competitive benefits, allowing immediate access to early rainfall and the associated release of soil nutrients prior to grass flushing (Ryan et al., 2017; February & Higgins, 2016). Detarioid species, slower growing with robust leaves, dense wood, and deep root

systems (Zhou et al., 2020; Timberlake & Calvert, 1993), frequently green-up before the rainy season has commenced. They may also retain their leaves for longer after the end of the rainy season, though the mechanisms of this behaviour are unclear (Giraldo & Holbrook, 2011; Kushwaha et al., 2011). Other species may only begin to produce foliage during the rainy season, creating a dense flush of low cost leaves during the mid-season peak of growth and dropping their leaves earlier as soil water content drops towards the end of the rainy season (Lasky et al., 2016). While species that green-up early gain a competitive advantage from having fully emerged leaves once the rainy season starts, they may be forced to prematurely drop their leaves to avoid excess water loss and maintain a positive carbon balance if seasonal rains occur much later than normal (Vinya et al., 2018), an occurrence which is becoming more common (Wainwright et al., 2021). It has been suggested that variation in phenological strategy among tree species is one mechanism by which increased species diversity increases resilience to, and maximises productivity in, water-limited woodland ecosystems (Stan & Sanchez-Azofeifa, 2019; Morellato et al., 2016).

Variation in seasonal patterns of foliage display affects broader ecosystem processes. Woodlands with a longer period of foliage display support a greater diversity and abundance of wildlife, particularly birds, but also browsing mammals and invertebrates (Cole et al., 2015; de Araujo et al., 2017; Morellato et al., 2016; Ogutu et al., 2013). As climate change reduces rainy season length and increases the intensity of drought events in African water-limited woodlands (Cook et al., 2020; Gore et al., 2019), woodlands with a diverse tree community may provide refugia for many animal species (Bale et al., 2002). The period of green-up is a key time for invertebrate reproduction (Prather et al., 2012) and herbivore browsing activity (Velasque & Del-Claro, 2016; Morellato et al., 2016). Pre-rain green-up provides a valuable source of moisture and nutrients for browsing herbivores before the rainy season (Makhado et al., 2018), and can moderate the understorey microclimate, increasing humidity, reducing UV exposure, moderating diurnal oscillations in temperature, and reducing ecophysiological stress which otherwise can lead to increased plant mortality during the dry season. Thus, understanding what drives variation in seasonal patterns of foliage display in tropical deciduous woodlands can provide valuable information on their vulnerability to climate change, and therefore better information to predict their future composition, extent and function.

In this study we investigate how tree species diversity and structure influence land surface phenology in seasonally dry tropical woodlands. We focus specifically on the lag between green-up/senescence and the onset/end of the rainy season, the magnitude of foliage display within the growing season, and the overall length of the growing season. We hypothesise that: (H_1) sites with greater species diversity will exhibit a longer growing season due to a higher diversity of phenological strategies; (H_2) in sites with greater species diversity the start of the growing season will occur earlier with respect to the onset of the rainy season due to an increased likelihood of containing species which

can green-up early; (H_3) sites with larger trees will have a longer growing season, as large trees can better access deep groundwater reserves outside of the rainy season; (H_4) sites dominated by detarioid species will experience earlier pre-rain green-up.

2 Materials and methods

2.1 Plot data

We used data on tree species diversity and composition from 619 sites surveyed as part of the Zambian Integrated Land Use Assessment Phase II (ILUA-II), conducted in 2014 (Mukosha & Siampale, 2009; Pelletier et al., 2018). Each site consisted of four 50×20 m (0.1 ha) plots positioned in a 500×500 m square around a central point (Figure 1), resulting in a total plot area per site of 4000 m^2. The original assessment contained 993 sites, which was filtered in order to define study bounds and to ensure data quality. Only sites with ≥50 stems ha^{-1} ≥10 cm DBH (Diameter at Breast Height) were included in the analysis, to ensure all sites represented woodlands with a relatively continuous canopy rather than open 'grassy savanna', which is considered a separate biome with different species composition and ecosystem processes governing phenology (Morellato et al., 2013; Keith et al., 2020).

Plots in the ILUA-II dataset sampled stems ≥10 cm DBH across the area of the whole plot, while stems <10 cm DBH were only measured within a 20×10 m (0.02 ha) nested subplot. We chose to use only stem measurements ≥10 cm DBH in this study, discarding measurements from the nested subplots. In woodland ecosystems with a relatively continuous canopy like those studied here, only the larger trees form the overstorey layer, with smaller trees existing within the understorey layer (Chidumayo, 2001). The signal from remotely-sensed measurements of land surface phenology is dominated by these larger trees which form the woodland canopy. We therefore reasoned that small stems would not be an important factor in determining measurements of land surface phenology. To further demonstrate the dominance of larger stems in our sites, we compared the per hectare basal area contribution of stems ≥10 cm with that of stems <10 cm DBH. We found that across all sites, the minimum proportional basal area contributed by stems ≥10 cm was 72%, while the median was 98%.

Sites with non-native tree species, e.g. *Pinus* spp. and *Eucalyptus* spp. were excluded, as these species may exhibit patterns of foliage display which differ markedly from that of native tree species assemblages (Broadhead et al., 2003). Of the 49 656 trees recorded, 97.9% were identified to species. Sites with >20% of trees not identified to species were discarded.

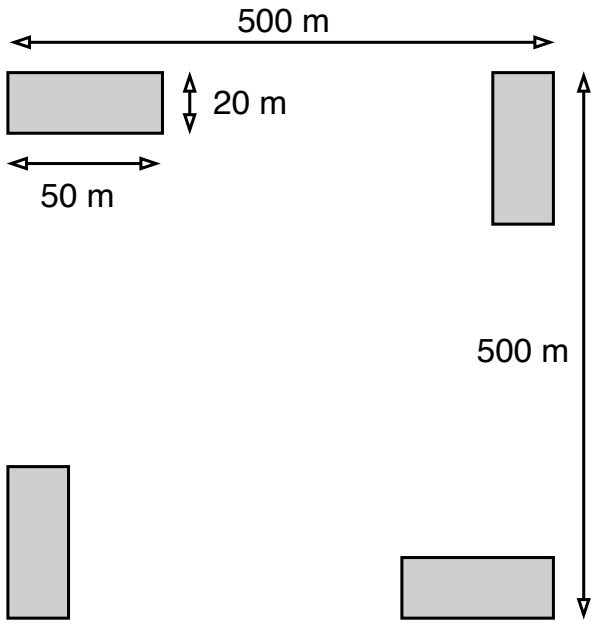

Figure 1: Schematic diagram of plot layout within a site. Each 50×20 m (0.1 ha) plot is shaded grey. Note that the plot dimensions are not to scale.

Within each plot, the species and basal area of all trees with at least one stem ≥10 cm DBH were recorded. Plot data were aggregated to the site level for all analyses to avoid pseudo-replication. Each site spans an area 500×500 m (0.25 km^2), matching that of the land surface phenology data. We excluded sites where plots differed appreciably in vegetation composition, to ensure that all sites used in statistical analysis were representative of the vegetation within the total 0.25 km^2 area of each site. Using the Bray-Curtis dissimilarity index on species basal area data (Faith et al., 1987), we calculated the mean pairwise compositional distance between plots within each site. Sites were discarded when the mean pairwise compositional distance among plots within the site was greater than the mean pairwise compositional distance of all plots across all sites. This resulted in a final dataset of 619 sites.

2.2 Vegetation composition and diversity

To describe variation in tree species composition across sites we used agglomerative hierarchical clustering on species basal area data (Kreft & Jetz, 2010; Fayolle et al., 2014) to assign sites to vegetation types. We excluded species with fewer than five records across all sites from this analysis, as very rare species can hinder meaningful cluster delineation. We used Ward's algorithm to define clusters (Murtagh & Legendre, 2014), based on the Bray-Curtis distance between pairs of sites. We determined the optimal number of clusters by maximising the mean silhouette width among clusters (Rousseeuw, 1987). We described the vegetation types represented by each cluster using

Dufrêne-Legendre indicator species analysis (Dufrêne & Legendre, 1997), which ranks species as the product of their relative frequency and their relative average abundance in each vegetation type. Four vegetation types were identified during hierarchical clustering. The mean silhouette value of the clustering algorithm was 0.64.

There was some spatial and climatic stratification in vegetation composition (Figure 2). Three miombo woodland types were identified, each with different sets of secondary species, but all dominated by detarioid species such as *Brachystegia* spp. and *Julbernardia* spp. (Table 1). Uapaca miombo is largely absent from the southwest of the country, occurring predominantly in higher rainfall regions to the north and east (Figure 3). Cryptosepalum miombo is found more in the southwest of the country, possibly representing the drier "Angolan miombo woodlands" described by White (1983). While Cryptosepalum miombo woodlands include *Cryptosepalum exfoliatum* as a secondary species, they should not be confused with Zambezian evergreen forests, which are dominated by Cryptosepalum (White, 1983). Julbernardia miombo is common in cooler areas and is more climatically restricted than the other miombo woodland types. Combretaceae woodlands match the description of small stature Zambezian woodlands, as described by Dinerstein et al. (2017) and Chidumayo (2001). These woodlands are not dominated by the same archetypal detarioid tree species as the other miombo woodland vegetation types. Combretaceae woodlands occur over a wide climatic range, and contain some of the warmest sites in our dataset in the southeast of the country. Median species richness and the range of species richness values per site is similar across vegetation types (Table 1).

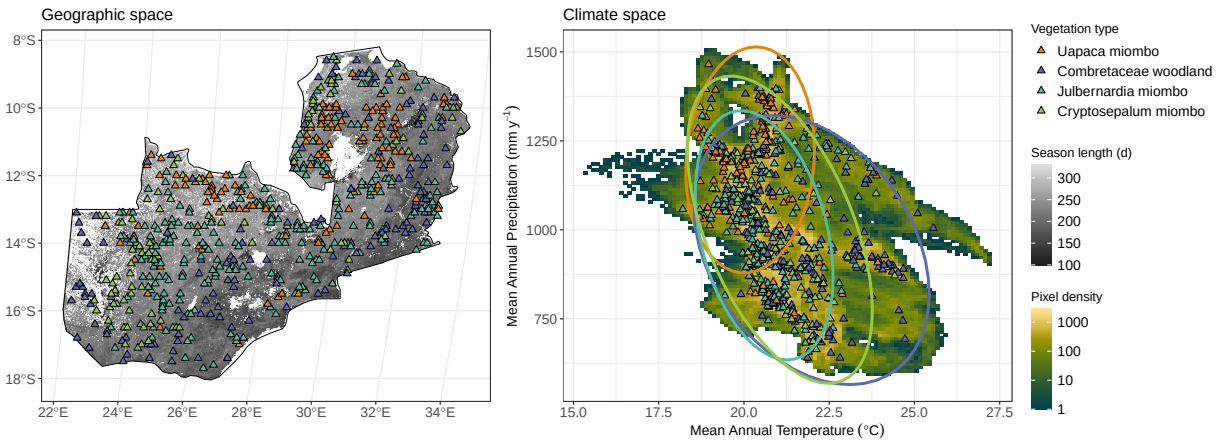

Figure 2: Distribution of study sites, within Zambia (left), and in climate space (right). Sites are shown as triangles, coloured according to vegetation type. Zambia is shaded according to mean growing season length during the period 2001 to 2021, estimated from the MODIS MCD12Q2 land surface phenology product, at 500 m spatial resolution (Friedl et al., 2022). Growing season length is masked by the MODIS MCD12Q1 land cover map from 2015 (Friedl & Sulla-Menashe, 2019), removing all pixels occurring in wetlands, croplands, water bodies, and urban areas. Climate space is represented by Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP), extracted from the WorldClim dataset at 30 arc second resolution (Fick & Hijmans, 2017). The shaded area in the right panel shows the climate space of Zambia, showing the density of pixels for given values of MAT and MAP. The ellipses in the right panel show the 95th percentiles of the climate space of each vegetation type.

Vegetation type	N sites	Richness	Indicator species	Indicator value
Uapaca miombo	135	17(7)	*Brachystegia longifolia*	0.393
			Uapaca kirkiana	0.384
			Marquesia macroura	0.278
Combretaceae woodland	144	14(5)	*Combretum molle*	0.258
			Lannea discolor	0.229
			Combretum zeyheri	0.212
Julbernardia miombo	244	17(6)	*Julbernardia paniculata*	0.556
			Brachystegia boehmii	0.540
			Pseudolachnostylis maprouneifolia	0.227
Cryptosepalum miombo	96	14(6)	*Brachystegia spiciformis*	0.582
			Cryptosepalum exfoliatum	0.285
			Guibourtia coleosperma	0.282

Table 1: Dufrêne-Legendre indicator species analysis for the vegetation type clusters, based on basal area weighted species abundances (Dufrêne & Legendre, 1997). The three species per cluster with the highest indicator values are shown alongside the median and interquartile range of site species richness and the number of sites within each cluster.

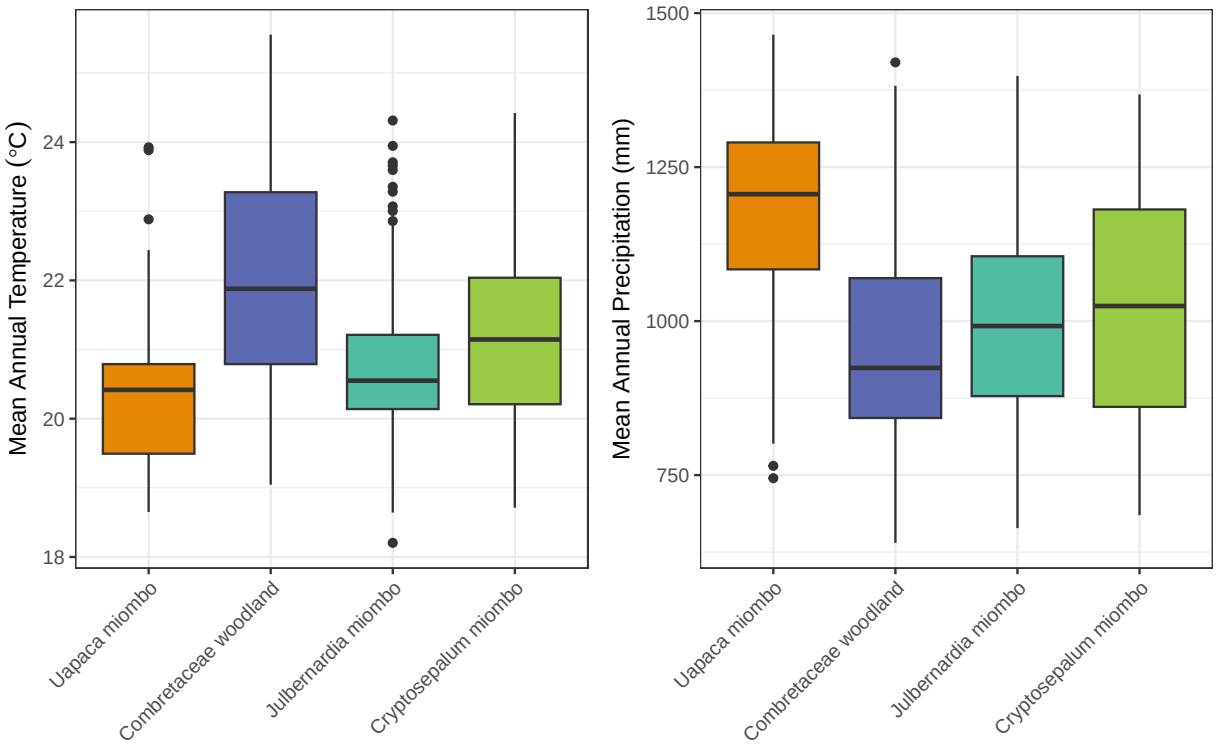

Figure 3: Mean Annual Precipitation and Mean Annual Temperature for each site, grouped by vegetation type. Climate data were extracted from the WorldClim dataset at 30 arc second resolution (Fick & Hijmans, 2017).

To describe species diversity in each site, we calculated the Shannon-Wiener index (H') from species basal area rather than individual abundance, as a measure of species diversity effectively weighted by species' contribution to canopy occupancy and thus the land surface phenological signal. H' was transformed to the first-order numbers-equivalent of H' ($^1D = e^{H'}$), which gives the equivalent number of equally common species that would result in a given value of H', also known as effective species richness (Jost, 2007). We use ^1D as the primary measure of species diversity in our statistical models, and is subsequently referred to as species diversity. To describe the abundance of Detarioideae species we calculated their proportional basal area. To describe average tree size, we calculated the quadratic mean of stem diameters per site. Quadratic mean diameter is exactly related to site basal area, unlike the arithmetic mean of diameter, and assigns greater weight to larger trees (Curtis & Marshall, 2000). It is thus a more appropriate descriptor of average stem size for this study, where the arithmetic mean would be biased by an abundance of small stems, despite their small contribution to overall canopy land surface phenological signal.

2.3 Remote sensing data

Precipitation time series data for each site was compiled from the GPM IMERG Final Precipitation L3 1 day V06 product, which has a pixel size of 0.1°(11.1 km at the equator) (Huffman et al., 2015). We used all available data from 2001 to 2021. There is no clear consensus on best practice for defining the limits of the rainy season (Guan et al., 2014). Here we followed the example of Stern et al. (1981) and Adole et al. (2018b), variations of which have been used in other studies of African savanna-woodland phenology (Mupangwa et al., 2011; Segele & Lamb, 2005). First, we determined the temporal bounds of each wet-dry season cycle within our study period of 2001 to 2021 for each site according to Ferijal et al. (2022), as the 14 day period with the lowest precipitation in each calendar year. Where multiple 14 day periods tied for lowest precipitation within a single calendar year, the later period was chosen.

The onset of the rainy season for each wet-dry season cycle was defined as the start of the first period of 10 days with more than 20 mm total rainfall, immediately followed by 20 days with more than 30 mm total rainfall (Tadross et al., 2005). With this rolling window approach we sought to identify the first sustained period where plant available soil moisture was increasing, i.e. where the average regional evaporation rate of ~1 mm per day was exceeded by rainfall (Campbell, 1996), while accounting for the stochastic nature of rainfall in our study at the start of the rainy season. We chose to relax the rainfall constraint from 2 mm d^{-1} in the first 10 day period, to 1.5 mm d^{-1} for the subsequent 20 day period, to account for variation in the temporal consistency of rainfall at the start of the rainy season in our study region. As opposed to a percentile of cumulative rainfall approach, our method is not affected by dry season storm-burst rainfall events, which, while contributing to overall cumulative rainfall, often do not generally have the capacity to initiate tree foliage production due to their transience (February & Higgins, 2016).

The end of the rainy season was defined as the start of the first period where fewer than four days within a 30 day period received more than 0.5 mm rainfall. Guan et al. (2014) compares other methods of estimating rainy season onset and end dates, and finds little functional difference between the method chosen here and other common methods. To validate our delimitation of the rainy season we checked that all season start and end dates occurred within 10 days of the dates where 10% and 95% of yearly cumulative rainfall were surpassed, respectively (Adole et al., 2018b).

To quantify seasonal patterns of leaf display at each site, we used the MODIS MCD12Q2 v6.1 land surface phenology product (Friedl et al., 2022). MCD12Q2 provides annual metrics describing land surface phenology, with a spatial resolution of ~500 m. The phenological metrics in MCD12Q2 are derived from the 2-band Enhanced Vegetation Index time series (1-2 day temporal resolution), with nadir Bidirectional Reflectance Distribution Function-adjusted surface reflectance (NBAR-EVI2).

There are a number of land surface phenology products derived from MODIS vegetation indices. MCD12Q2 was chosen here as it has been used effectively in other studies in deciduous African woodlands to define the growing season (Begue et al., 2014; Adole et al., 2018a). Additionally, a previous comparison of MODIS-derived land surface phenology products showed that MCD12Q2 out-performed other products in predicting the start of the growing season in relation to ground observations (Peng et al., 2017).

All sites were determined to have a single annual growing season according to the MCD12Q2 "NumCycles" metric. We used all years of data from 2001 to 2021. We used the "Greenup" and "Dormancy" metrics to define the growing season as the period when the EVI time series exceeds 15% of the EVI amplitude for a given growing season (Figure 4). We used the "Maturity" and "Senescence" metrics, defined as the dates bounding the period where the EVI time series exceeds 90% of the EVI amplitude, to define the end of the green-up period and the start of the senescence period, respectively. We used these dates to calculate the length of the green-up period and senescence period. We calculated "pre-rain green-up" as the number of days between the onset of the growing season and the onset of the rainy season, for each year of available data. Similarly we calculated "senescence lag" as the number of days between the end of the rainy season and the end of the growing season. To aid interpretation of statistical models, we reversed the sign of the pre-rain green-up measurements, so that larger values indicate earlier pre-rain green-up. As senescence generally occurred after the end of the rainy season, we did not reverse the sign of senescence lag, so larger values indicate later senescence.

Daily total precipitation from the GPM IMERG product was separated into three periods of relevance to different phenological metrics: precipitation during the growing season, precipitation in the 30 day period before the onset of the growing season (pre-green-up precipitation), and precipitation in the 30 day period before the onset of senescence at the end of the growing season (pre-senescence precipitation) (Figure 4).

Temperature time series data for each site was compiled from the ERA5-Land hourly data, using the 2 m air temperature variable at 0.1°(11.1 km at the equator) (Muñoz-Sabater et al., 2021). We aggregated these data to the maximum temperature for each day over the period 2001 to 2021. We then calculated cumulative temperature (degree days) during the 30 day pre-green-up period, 30 day pre-senescence period, and the growing season period, as with the precipitation data. Cumulative temperature has been shown in previous studies to be an important cue driving patterns of leaf display in more temperate systems (Archibald & Scholes, 2007; Michelson et al., 2017; Gárate-Escamilla et al., 2020). While the spatial scales of the climate data (0.1°) and land surface phenology data (500 m) do not match we believe this does not present a problem for our analyses. Firstly, because temperature and rainfall data are expressed in our analyses as cumulative

values across longer time periods, for example cumulative rainfall over the 30 days prior to green-up, we do not expect systematic spatial variation in these aggregated values within each 0.1° pixel, especially when considering multiple years of data. Secondly, the distance among sites is much greater than the resolution of the climate data. Any variation in temperature or rainfall within pixels is likely to be less than that among sites.

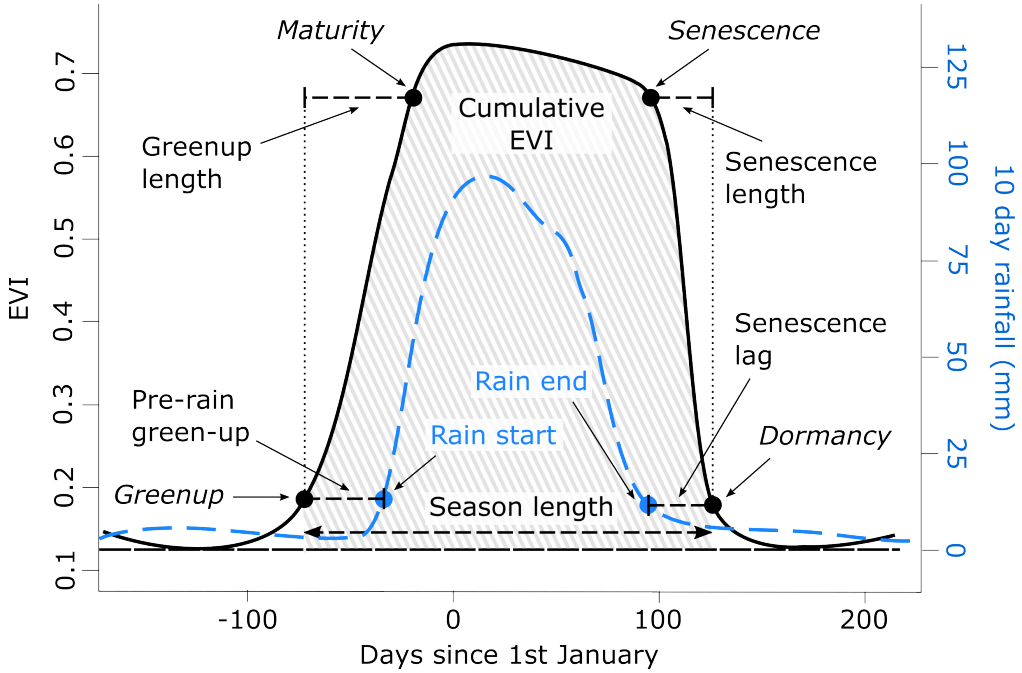

Figure 4: Schematic diagram of hypothetical splined NBAR-EVI2 time series (black curve), from which metrics provided by the MCD12Q2 product are derived (black circles), Adapted from Gray et al. (2022). Cumulative EVI is denoted by the shaded area under the EVI curve for a given growing season, bounded by the "Greenup" and "Dormancy" dates. The blue curve shows a hypothetical splined 10 day rolling total rainfall time series, derived from the GPM IMERG product. Blue circles indicate the start and end of the rainy season as defined by our algorithm. Dashed black lines indicate the derived phenological metrics used in this study. In this hypothetical example, "Greenup" occurs in advance of the start of the rainy season, and "Dormancy" occurs after the end of the rainy season, reflecting the condition of 72.7% (8451/11 625) of the yearly data in our dataset. In 26.7% (3106/11 625) of cases, dormancy occurred after the end of the rainy season and green-up occurred after the start of the rainy season. In 0.6% (68/11 625) of cases, dormancy occurred before the end of the rainy season.

2.3.1 Statistical modelling

Linear mixed effects models were used to investigate the effect of tree species diversity (effective number of species), species composition (relative abundance of detarioid species), and woodland structure (quadratic mean of stem diameter) on each of the six phenological metrics (cumulative

EVI, season length, length of green-up period, length of senescence period, pre-rain green-up, senescence lag). We specified a maximal model structure including the fixed effects of species diversity, quadratic mean of stem diameter, relative abundance of detarioid species, precipitation and cumulative temperature, the latter two of which have been shown by previous studies to strongly influence patterns of foliage display, including green-up and senescence (Whitecross et al., 2017; Adole et al., 2019). For models of growing season length and cumulative EVI we used cumulative rainy season precipitation and temperature; for pre-rain green-up and length of green-up period we used cumulative pre-green-up precipitation and temperature; for senescence lag and length of senescence period we used cumulative pre-senescence precipitation and temperature. All models included a random intercept term for site to account for yearly repeated measurements of site land surface phenology. Fixed effects in each model were standardised to Z-scores prior to modelling to allow comparison of slope coefficients within models.

To determine the magnitude and direction of each fixed effect on each phenological metric, we compared standardised effect sizes extracted from models re-estimated using Maximum Likelihood. For each fixed effect we calculated the 95% confidence interval of the effect size as 1.96× the standard error of the parameter estimate (Zuur et al., 2010). All statistical analyses were conducted in R version 4.0.2 (R Core Team, 2020).

3 Results

The majority of sites experienced pre-rain green-up, with the site mean date of green-up occurring in advance of the mean onset of the rainy season in 498/619 sites. Across all sites, the mean lag between green-up and the onset of seasonal rains was 14±20.2 days (±1 standard deviation). Linear mixed effects models effectively explained pre-rain green-up (R^2_m=0.45, R^2_c=0.65), cumulative EVI (R^2_m=0.21, R^2_c=0.72), green-up length (R^2_m=0.20, R^2_c=0.38) and season length (R^2_m=0.14, R^2_c=0.63), while senescence length (R^2_m=0.01, R^2_c=0.20) and senescence lag (R^2_m=0.03, R^2_c=0.30), were poorly explained. Fixed effects accounted the majority of total variance explained in models for pre-rain green-up, season length and green-up length, while the random effect of site explained most of the variance in cumulative EVI (Table S1).

We compared standardised fixed effect sizes for each phenological metric to determine the strength and direction of their influence (Figure 5). Tree species diversity exhibited positive effects on season length (β=4.7±0.70, standardised coefficient ± standard error) (H_1) and pre-rain green-up (β=1.0±0.39) (H_2). Average tree size, measured by the quadratic mean of stem diameter per site, was a significant predictor of pre-rain green-up (β=2.0±0.38) and green-up length (β=1.0±0.33), associated with early pre-rain green-up and a longer green-up period (H_3). Sites with larger trees

also experienced later senescence (β=0.8±0.67). The proportional basal area of detarioid species was a significant predictor of pre-rain green-up (β=1.0±0.40), and season length (β=1.7±0.71) (H_4).

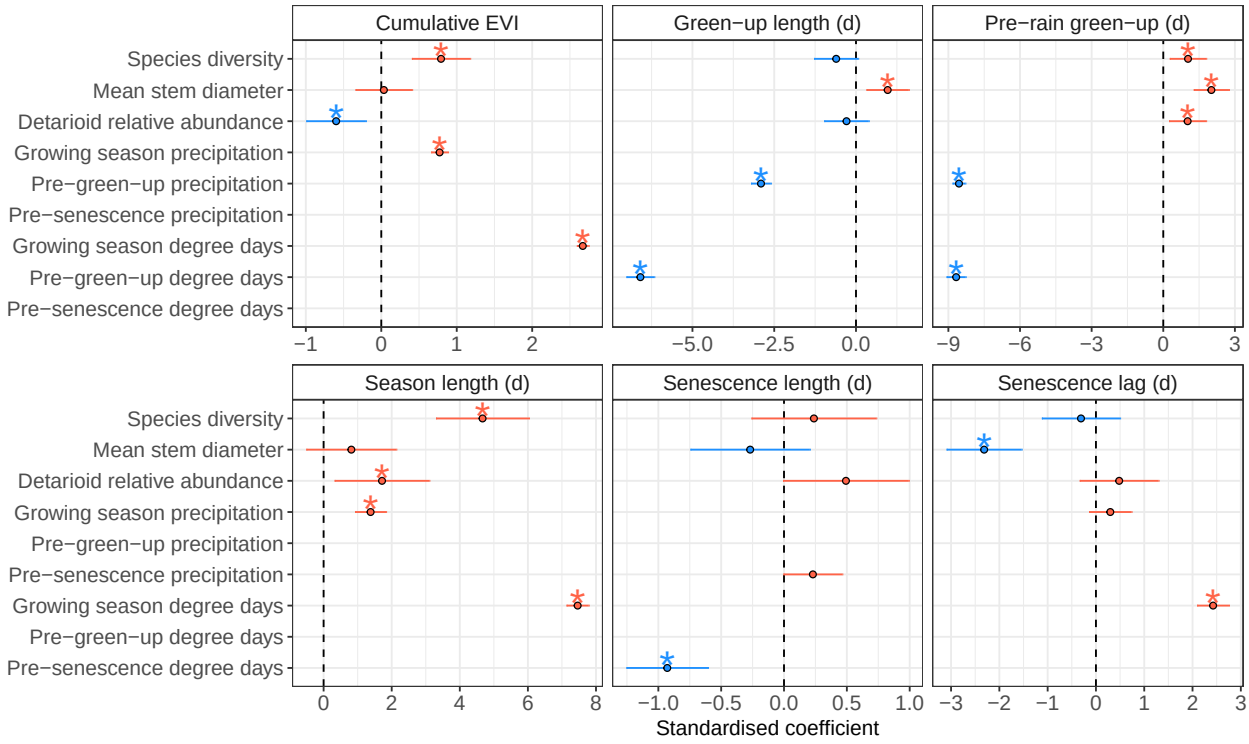

Figure 5: Standardised fixed effect coefficients (dots) with 95% confidence intervals (whiskers) for models of each phenological metric (panels). Estimates where the 95% confidence interval does not overlap zero are considered to be significant and are marked by asterisks. Temperature (degree days) and precipitation data were summed over different periods most relevant to each phenological metric. Green-up length and pre-rain green-up used data from the 30 day pre-green-up period, senescence length and senescence lag used data from the 30 day pre-senescence period, cumulative EVI and season length used data from the growing season period.

4 Discussion

We have demonstrated clear effects of tree species diversity, composition and structure on various metrics of land surface phenology in seasonally dry tropical woodlands across Zambia. Both tree species diversity and the proportional basal area of trees from the Detarioideae (subfamily of Fabaceae), were associated with a longer growing season and with earlier pre-rain green-up. Our models partition the effects of species diversity and detarioid relative abundance, suggesting that while some of the positive species diversity effect is due to niche complementarity, i.e. a true diversity effect, some is due to the increased likelihood of containing species able to green-up earlier, i.e. a mass-ratio effect (Grime, 1998; Tilman et al., 2014). Our study lends support for a gen-

eral positive effect of tree species diversity on ecosystem function in southern African seasonally dry tropical woodlands, measured through leaf display (Richardson et al., 2009), which aligns with other recent studies in the region (Godlee et al., 2021; McNicol et al., 2018; Shirima et al., 2015). Our results highlight the important role of detarioid species in southern African woodland productivity: we show that increasing abundance of these species increases both early season productivity and overall growing season length.

The basal area of detarioid species had a positive effect on pre-rain green-up. Our results suggest a mass-ratio effect in the pre-rain green-up of Zambian deciduous woodlands (Grime, 1998), whereby a dominant functional group of trees with particular traits and life history strategy is able to green-up in advance of seasonal rains and drive longer growing seasons. Given their tendency to create deep root networks which provide effective water and non-structural carbohydrate storage (Zhou et al., 2020; Timberlake & Calvert, 1993), and their high wood density which confers embolism-resistance to the tree hydraulic system (Hoffmann et al., 2011; Hacke et al., 2001; Chave et al., 2009), we suggest that compared to other co-occurring taxonomic groups, detarioid species are better equipped to green-up before seasonal rainfall begins (Vinya et al., 2018). In our analysis we accounted for the effect of tree size on pre-rain green-up, which generally correlates with rooting depth, and still found an effect of detarioid abundance on pre-rain green-up, implying a true effect of detarioid species not linked to tree size. While pre-rain green-up is a risky strategy, it may provide a competitive advantage for detarioid species, allowing them to take advantage of early rainfall and associated soil nutrient release (February & Higgins, 2016).

While at present the ability to green-up prior to the rainy season provides a competitive advantage to detarioid species by extending the period of productivity, it is unclear whether this behaviour will continue to provide a benefit under a changing climate, where the timing of the rainy season is expected to shift, becoming more erratic and shorter overall (Shongwe et al., 2011; Pohl et al., 2017; Wainwright et al., 2021). Given the dominance of detarioid species in miombo woodlands across southern Africa, decreased productivity of this group due to a mismatch between leaf display and seasonal rainfall may affect the future composition, structure and functioning of these woodlands, potentially leading to a shorter stature, lower biomass and lower productivity ecosystem.

Environmental variables had consistently strong effects on phenological metrics, and confirm previous research. Greater rainfall within the rainy season led to a longer growing season and greater cumulative EVI, matching our expectations that increased water availability allows for greater foliage production and builds groundwater reserves allowing for a longer growing season (Adole et al., 2018b). Surprisingly, greater rainfall in the 30 days leading up to the start of the growing season was associated with later green-up with respect to the onset of the rainy season. We suggest this may be the result of large amounts of rainfall kick-starting foliage production in the absence of

a pre-rain green-up effect in some sites, and may represent cases where grasses drive the start of growing season land surface phenology signal. This inability to discriminate between the grassy component and the tree canopy component of the phenological signal highlights one of the principle drawbacks with space-borne land surface phenology to characterise patterns of vegetation leaf display (Archibald & Scholes, 2007). Hotter days were associated with shorter periods of senescence and green-up, but ultimately a longer growing season and greater overall productivity. In the case of green-up length, this effect may imply a temperature trigger on leaf display, as is seen in temperate woodland ecosystems (Flynn & Wolkovich, 2018). In the case of senescence, hotter days at the end of the growing season are expected to increase photorespiration and ultimately result in a negative leaf carbon balance, triggering leaf loss (Warren et al., 2011; Mariën et al., 2019). This study provides a glimpse into how climate change, particularly warming (Arias et al., 2021) and increased rainfall seasonality (Wainwright et al., 2021), could affect leaf phenology in the future in southern Africa. Future temperature increases in miombo woodlands, particularly high temperatures at the start and end of the rainy season, could accelerate green-up and senescence processes. Similarly, a reduction in precipitation during the growing season could reduce growing season length and overall productivity. Future studies could explore further how climate extremes affect land surface phenology, ideally in combination with measurements of species composition and ecosystem structure, which this study has shown are also important drivers of ecosystem function.

The end of the growing season came later with respect to the end of the rainy season in plots with larger mean stem diameter, though our model had low explanatory power. Cho et al. (2017) found that tree cover, measured by MODIS Leaf Area Index (LAI) data, had a significant positive effect on end of growing season date in tropical dry woodlands in South Africa. Similarly, Guan et al. (2014) found at continental scale across Africa that the end of the growing season came later with respect to the end of the rainy season in areas where tree cover was higher. Both these previous studies posit that the observed effect of tree cover on end of growing season date might indicate the presence of larger trees capable of accessing deeper groundwater reserves or holding stem-water reserves after the rainy season ends and surface soil moisture is depleted. Our study lends further support for this suggestion by directly testing the effect of tree size, rather than tree cover.

Our best models predicting the length of the senescence period and the end of growing season lag did not explain much of the variance in these phenological metrics. Short term oscillations in soil moisture driven by localised rainfall events, and the condition of ground cover vegetation may be responsible for driving the length of the senescence period, hence the wide spatio-temporal variability of this phenological metric and the poor fit of our statistical models. Most of the variance explained by our models of senescence period length and senescence lag came from the random effect of site, implying some unmeasured inter-site variation. Grass productivity is more reactive to short-

term changes in soil moisture than tree activity, and may oscillate within the senescence period (Archibald & Scholes, 2007). This may explain the lack of a strong growing season precipitation or tree diversity signal for senescence lag and length of the senescence period in our models.

Other studies, both globally and within southern African woodlands, have largely ignored patterns of senescence, instead focussing on patterns of green-up (Gallinat et al., 2015). Most commonly, studies of senescence simply correlate the decline of rainfall with senescence (Stevens et al., 2016; Guan et al., 2014), but our best model suggests that temperature is a stronger determinant of the end of the growing season than precipitation. We suggest that hotter days at the end of the growing season might accelerate senescence through tissue damage and embolism (Cho et al., 2017), resulting in a shorter period of senescence. In temperate ecosystems, which experience autumn senescence, lower night time temperatures have been shown to increase the rate of senescence and thus decrease senescence period length (Michelson et al., 2017; Gárate-Escamilla et al., 2020). In these water-limited and hot systems however, it seems hotter temperatures are the main driver of senescence. Hotter days prior to senescence appear to delay the onset of senescence with respect to the end of the rainy season, and higher temperatures across the growing season were associated with a longer growing season. Thus, while climate warming could accelerate the process of senescence, it may also delay the senescence period with respect to the end of the rainy season.

Alternatively, Zani et al. (2020) suggests that in resource-limited environments, senescence times may largely be set by preceding photosynthetic activity and sink-limitations on growth. For example, limited nutrient supply may prohibit photosynthesis late in the season if the preceding photosynthetic activity has depleted that supply. Reich et al. (1992) suggested that there are many direct constraints on leaf life-span such as drought and herbivory, especially in the seasonally dry tropics, which would lead to timing of senescence being set largely by the time of bud-burst. Our study indirectly corroborates this theory, with the finding of a moderate negative correlation between pre-rain green-up and senescence lag across all vegetation types indicating that later green-up allows later senescence (Figure S1).

We found positive effects of tree size (site quadratic mean diameter) on pre-rain green-up and green-up length, but negative effects on senescence lag. Our results agree with previous studies that the increased rooting depth of large trees allows them to access deep ground-water reserves, conferring resilience to inter-annual variation in patterns of seasonal rainfall (Holdo et al., 2017). While detarioid species in these woodlands tend to grow to large sizes, our result of a significant effect of tree size alongside an effect of detarioid abundance on pre-rain green-up infers particular traits beyond tree size in the detarioid species that drive pre-rain green-up.

Our finding that species diversity increases growing season length and cumulative EVI in seasonally dry tropical woodlands provides an example of a mechanism by which species diversity increases

ecosystem function, a pattern observed previously in other studies of southern African woodlands (Godlee et al., 2021; McNicol et al., 2018; Shirima et al., 2015), and globally in other biomes (van der Plas, 2019; Tilman et al., 2014). Our findings provide earth system modellers with an insight to better understand how changes in the inter-related variables of species diversity, composition and structure affect one measure of ecosystem function (land surface phenology). Future studies should aim to disentangle these effects further, possibly in an experimental context. Incorporating predictions of biotic composition and its change over time into earth system models has been limited until recently for two main reasons. Firstly, there are large uncertainties in the effects of biodiversity on ecosystem function, e.g. gross primary productivity (GPP) (Ahlstrom et al., 2015). Secondly, until recently there has been a major paucity of ground data on community composition, and a lack of appropriate remote-sensing data to scale up to larger areas (van Bodegom et al., 2011). Our study comes at a pertinent time where plot-based vegetation monitoring networks are now sufficiently widespread to robustly test hypotheses and generate theory on the effects of community composition on ecosystem function across environmental gradients (ForestPlots.net et al., 2021; SEOSAW, 2020). Additionally, recent advances in remote sensing of functional diversity from hyperspectral data, combined with the imminent deployment of space-borne imaging spectrometers by multiple space agencies (Cawse-Nicholson et al., 2021; Rast et al., 2021), will soon allow community composition to be mapped at large spatial scales (Wallis et al., 2024; Cavender-Bares et al., 2020) and utilised by earth system modellers. Our study serves as an example of the kinds of advancements in ecological understanding relevant to earth system modelling that can be made by integrating abundant ground data and remote sensing data.

5 Conclusion

We explored how tree species diversity, composition and structure of seasonally dry tropical woodlands influence land surface phenology across Zambia. We showed that species diversity drives longer growing seasons and promotes earlier pre-rain green-up across woodlands in the miombo ecoregion. The abundance of Detarioideae species (subfamily of Fabaceae) had a positive effect on pre-rain green-up and growing season length, supporting suggestions from previous studies of their important role in driving pre-rain green-up in southern African miombo woodlands. Finally, we found that larger trees drive earlier pre-rain green-up supporting previous research suggesting that deep roots and persistent carbohydrate storage allows for precocious leaf display.

Our results lend further support to an already well established corpus of study on the positive effect of species diversity on ecosystem function. Additionally, our results provide evidence for earth-system modellers, demonstrating the importance of structure and diversity in determining patterns

of land surface phenology. As reliable data on ecosystem structure, particularly tree size, become available across larger spatial scales and at higher spatial resolution, we hope that these data can be explored in models of land-atmosphere mass and energy exchange to improve their predictive skill under a changing climate.

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6 Supplementary material

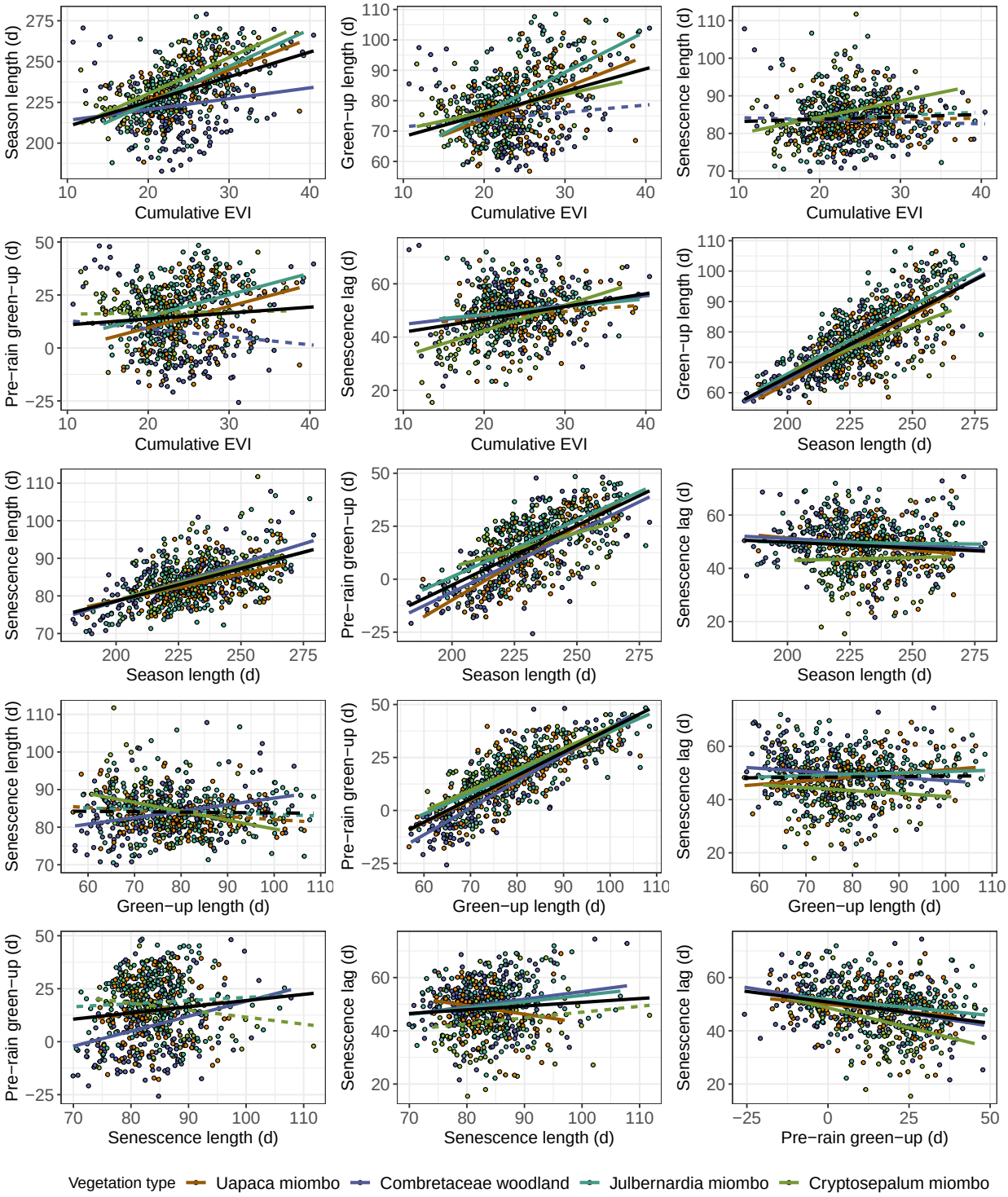

Figure S1: Scatter plots showing pairwise comparisons of the six phenological metrics used in this study, extracted from the MODIS MCD12Q2 product (Friedl et al., 2022). Points represent study sites and are coloured by vegetation type. Linear regression line of best fit for all sites is shown as a black line, while linear regressions are shown for each vegetation type as coloured lines. Non-significant linear regression fits ($p<0.05$) have dashed lines. Units of 'd' are the number of days.

Table S1: Performance of models for each phenological metric, showing standardised parameter estimates (95% confidence interval), and goodness of fit statistics. ΔAIC is the difference in AIC between the full model and a null random effects only model. R^2_m and R^2_c refer to the marginal and conditional R^2, respectively. ICC is the Intra-Class Correlation statistic, which shows how strongly yearly data within each site are correlated. Parameter estimates are marked by an asterisk where the 95% confidence interval does not overlap zero. Models for different phenological metrics used precipitation and degree days from different relevant periods but these values have been combined into single columns in this table. Green-up length and Senescence length used the pre-green-up period, Senescence length and Senescence lag used the pre-senescence period, Cumulative EVI and Season length used the growing season period.

Response	Intercept	Precipitation	Degree days	Species diversity	Stem diameter	Detarioid abundance	ΔAIC	R^2_m	R^2_c	ICC
Cumulative EVI	24.64(0.858)*	0.77(0.111)*	2.67(0.078)*	0.79(0.386)*	0.03(0.375)	-0.6(0.395)*	3713	0.21	0.72	0.65
Season length	235.04(3.044)*	1.38(0.456)*	7.46(0.325)*	4.67(1.364)*	0.81(1.321)	1.72(1.391)*	1893	0.14	0.63	0.57
Green-up length	76.59(1.517)*	-2.9(0.301)*	-6.59(0.425)*	-0.61(0.673)	0.97(0.647)*	-0.29(0.681)	1111	0.20	0.38	0.23
Senescence length	83.14(1.125)*	0.23(0.234)	-0.93(0.324)*	0.24(0.496)	-0.27(0.475)	0.49(0.5)	38	0.01	0.20	0.19
Pre-rain green-up	11.37(1.72)*	-8.56(0.268)*	-8.67(0.399)*	1.04(0.763)*	2.01(0.737)*	1.02(0.776)*	4410	0.45	0.65	0.35
Senescence lag	49.55(1.796)*	0.3(0.44)	2.43(0.329)*	-0.31(0.81)	-2.31(0.777)*	0.48(0.816)	219	0.03	0.30	0.28