Drought resistance increases from the individual to the ecosystem level in highly diverse neotropical rain forest: a meta-analysis of leaf, tree and ecosystem responses to drought

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Abstract. The effects of future warming and drying on tropical forest functioning remain largely unresolved. Here, we conduct a meta-analysis of observed drought responses in neotropical humid forests, focused on carbon and water exchange. Measures of leaf, tree and ecosystem scale performance were retrieved from 145 published studies conducted across 232 sites in neotropical forests. Differentiating between seasonal and episodic drought we find that; (1) during seasonal drought, the increase of atmospheric evaporative demand and a decrease of soil matric potential results in a decline of leaf water potential, stomatal conductance, leaf photosynthesis and stem diameter growth while leaf litterfall and leaf flushing increase. (2) During episodic drought, we observe a further decline of stomatal conductance, photosynthesis, stem growth and, in contrast to seasonal drought, also a decline of tree daily transpiration. Responses of ecosystem scale processes, productivity and evapotranspiration, are of a smaller magnitude and often not significant. Furthermore, we find that the magnitude and direction of a drought-induced change in photosynthesis, stomatal conductance and transpiration reported in a study is correlated to study-averaged wood density. Although wood density is often not functionally related to plant hydraulic properties, we find that it is a good proxy of hydraulic behaviour and can be used to predict leaf and tree scale responses to drought. We present new insights into the functioning of tropical forest in response to drought and present novel relationships between wood density and tropical tree responses to drought.

1 Introduction

The neotropical rainforests of South and Central America, with the Amazon Basin at its centre, cover the largest tract of tropical forest on Earth. As such, these forests are a crucial component of the regional and global climate system as a source of convective heat and moisture, driving atmospheric moisture transport and precipitation patterns (Poveda and Salazar, 2004; Zemp et al., 2014). General circulation models project that South and Central America will warm by 2 °C to 5 °C in the coming decades under the business as usual emission scenario (Marengo et al., 2010). Furthermore, seasonal drought is expected to become more severe (Boisier et al., 2015; Malhi et al., 2009; Marengo et al., 2010). Undisturbed old growth forest

in the Amazon Basin has increased in aboveground biomass since the 1980's, acting as a substantial sink of atmospheric carbon (Feldpausch et al., 2016; Phillips et al., 2009). However, recent drought events appear to have at least temporarily reversed the Amazon carbon sink through reduced productivity (Gatti et al., 2014; Yang et al., 2018b), elevated tree mortality (Feldpausch et al., 2016; Phillips et al., 2009) and increased emissions from fire (Aragão et al., 2018; Van Der Laan-Luijkx et al., 2015;

35 Van Der Werf et al., 2008). Furthermore, the integrity of neotropical forests may be threatened by unforeseen feedback mechanisms triggered by drought and deforestation (Khanna et al., 2017; Zemp et al., 2017). These vegetation-atmosphere feedbacks can reduce atmospheric moisture recycling and increase carbon emissions, which further amplifies forest loss and global climate change (Cox et al., 2000, 2004; Davidson et al., 2012; Erfanian et al., 2017; Exbrayat et al., 2017; Malhi et al., 2009).

Despite the critical role of neotropical forests in driving future climate scenarios, there are large uncertainties surrounding the sensitivity of these forests to drought. Uncertainties are partly the result of the biological diversity found in neotropical forests as the magnitude and direction of a response to drought is found to be strongly dependent on the species measured (Bonal et al., 2000a; Domingues et al., 2014). Also, uncertainties arise as droughts differ in length, periodicity and severity (Bonal et al.,

45 2016; Marengo et al., 2011; Meir et al., 2018). Finally, ecophysiological responses to drought occur on a multitude of spatial and temporal scales. These responses range from the almost instant closure of the stomata on a single leaf, to large scale tree mortality that has persistent effects on many ecosystem processes (Brando et al., 2008; Rowland et al., 2015b, 2015a). Currently, there is no quantitative overview of how neotropical forests respond to different intensities of drought, from the leaf level up to the entire ecosystem. Below we formulate three key issues that guide our meta-analysis.

50 **1.1 What type of droughts occur in neotropical forests?**

Here, we differentiate three types of drought that differ in periodicity and severity: seasonal drought, episodic drought and multi-year drought. Seasonality in precipitation is widespread in neotropical forests. Tropical humid forests loose roughly 100 mm of water every month through evapotranspiration (da Rocha et al., 2004; Shuttleworth, 1988). Months receiving less than 100 mm of rainfall will thus result in a precipitation deficit, these months are generally referred to as dry season months

55 (Aragão et al., 2007; Sombroek, 2001). Seasonal droughts are by definition periodic and trees are generally found to be adapted to such a seasonal decline in precipitation (Brando et al., 2010; Goulden et al., 2004; Hutyra et al., 2007).

Episodic droughts, on the other hand, are caused by anomalous climatic conditions, primarily those imposed by strong El Niño Southern Oscillations (ENSO) and tropical North Atlantic sea surface temperature anomalies (Marengo et al., 2011). In the

60 neotropics, episodic droughts often coincide with record breaking air temperatures (Jiménez-Muñoz et al., 2016; Lee et al., 2013; Panisset et al., 2017). Elevated air temperature can directly impact plant function through physiological heat stress (Doughty, 2011; Doughty and Goulden, 2009a) but it also drives a non-linear increase in atmospheric vapour pressure deficit (VPD). This increase of evaporative demand during drought can amplify drought conditions through increased

evapotranspiration, accelerating soil drying (Jung et al., 2010) and increasing the risk of hydraulic failure (Mcdowell et al.,
2008). The amplification of plant drought stress during episodic drought through the interaction of soil drying, high air
temperatures and evaporative demand have been termed "hotter droughts" (Allen et al., 2015; Breshears et al., 2013) and are
expected to become more frequent and severe with climate change.

Multi-year droughts are defined as a more permanent reduction of precipitation spanning years to decades. Long term records
of river discharge and oxygen isotopes in tree rings indicate that neotropical forests experienced several multi-year droughts
in the 20th century, notably in the 1960s (Brienen et al., 2012; Marengo et al., 2011; Richey et al., 1989). To date, the effect of
prolonged rainfall reduction on leaf, tree and ecosystem functioning have only experimentally been assessed in two throughfall
exclusion experiments at Tapajós and Caxiuanã in the eastern Amazon (Fisher et al., 2006; Meir et al., 2009; Nepstad, 2002).
The results from the Tapajós and Caxiuanã experiments have been previously synthesised (e.g. Meir *et al.*, 2009, 2018; da
Costa *et al.*, 2010a) and much of our knowledge about leaf, tree and ecosystem scale responses to multi-year droughts in
tropical forests originates from these experiments. Therefore, and because of the low number of replicates (i.e., 2) of such
experiments, this meta-analysis will focus only on the effects of seasonal and episodic drought on leaf, tree and ecosystem
functioning.

1.2 How is drought impacting leaf, tree and ecosystem scale processes?

On the leaf scale, seasonal and episodic drought are often found to result in a downregulation of stomatal conductance; the
ease by which CO_2 and water vapor can diffuse between the atmosphere and the leaf intercellular spaces through the stomates
(Hogan et al., 1995; Huc et al., 1994). The most recent evidence suggests that stomates progressively close in response to a
decline in leaf water potential (ψ_l) (Buckley, 2019; Choat et al., 2018; Drake et al., 2017; Martin-StPaul et al., 2017). Here,
we focus specifically on how drought-induced changes in ψ_l, the water potential gradient and the different conductance's
along the hydraulic pathway are driving the observed drought-induced changes in productivity and transpiration. During steady
state transpiration, transpiration at the leaf level (mol H_2O m^{-2} s^{-1}) is given by:

$$E = G_c \frac{VPD}{P} \qquad (1)$$

where G_c is the leaf-area specific crown conductance to water vapor (mol H_2O m^{-2} s^{-1}), VPD is the atmospheric vapor pressure
deficit (kPa) and P is the atmospheric pressure (kPa). The crown conductance itself can be calculated using the resistance
subtraction method:

$$G_c = \frac{1}{(1/g_s + 1/g_b)} \qquad (2)$$

where g_s is the stomatal and g_b the boundary layer conductance to water vapor (mol H_2O m^{-2} s^{-1}). Similar to leaf transpiration,
the transpiration flow through the tree can be described by:

$$J = k_{sl}(\psi_s - \psi_l) \qquad (3)$$

where J is the sapwood-area specific transpiration rate (i.e. sap flux density, g H_2O m^{-2} s^{-1}), k_{sl} the sapwood-area specific soil to leaf hydraulic conductance (g H_2O m^{-2} MPa^{-1}) and ψ_s the soil water potential in the root-zone (MPa). During steady state transpiration, the flow of water through the tree equals the transpiration from the total leaf surface area of the tree, so that:

$$J = E \times M_w \frac{A_l}{A_s} \qquad (4)$$

where M_w is the molar mass of water (~18 g mol^{-1}) and A_l and A_s are the total leaf and sapwood area (m^2) of the tree, respectively. Equation 1 describes the vapor phase transport of water through the leaf stomates from the leaf to the atmosphere, while Equation 3 describes the liquid phase water transport from the root to the leaf through the xylem sapwood. During drought, k_{sl} declines sharply as a result of reduced hydraulic conductance of a drier soil as well as of a reduced hydraulic conductance of the xylem as a result of xylem embolism (e.g. Fisher et al., 2006). It follows that the decline of k_{sl} should be balanced by a decline in G_c that is achieved by progressive stomatal closure (Meinzer et al., 1995). Nonetheless, Equation 1 and 3 also show that transpiration can stay the same, increase or decrease during drought, depending on whether a decline in k_{sl} and G_c is compensated for by an increase of the water potential gradient ($\psi_s - \psi_l$) or evaporative demand (VPD).

Progressive stomatal closure does not only constrain transpiration but also the diffusion of CO_2 into the leaf, limiting leaf photosynthesis. In neotropical humid forests, the stomatal conductance response to drought is generally larger than the decline in leaf photosynthesis, resulting in an increase in intrinsic water use efficiency (iWUE) (Bonal et al., 2000a; Santos et al., 2018). It is unclear how leaf-scale processes respond to drought in neotropical humid forest, with some studies reporting strong reductions in stomatal conductance, transpiration and photosynthesis during seasonal and episodic drought (e.g. Hogan et al., 1995a; Huc et al., 1994; Sendall et al., 2009; Wolfe et al., 2016) while others report no significant change in stomatal conductance and photosynthesis and even an increase of transpiration (e.g. Allen and Pearcy, 2000; Domingues et al., 2014; Fisher et al., 2006).

Leaf scale responses to drought can propagate to the tree scale, with reduced growth of the stem and new leaves, increased leaf shedding and litter fall and reduced tree daily transpiration (Brum et al., 2018; Doughty et al., 2015; Fontes et al., 2018; Hofhansl et al., 2014; Phillips et al., 2009). Furthermore, the combined drought response of all individual trees in the ecosystem contributes to the observed ecosystem scale response to drought. Reduced leaf photosynthesis and leaf and stem growth can result in a decline of gross primary productivity (GPP) and consequently a decline of net primary productivity (NPP) while reduced tree daily transpiration might result in a decline of ecosystem evapotranspiration. Moreover, increased leaf litterfall in response to drought can boost microbial respiration and result in an increase of ecosystem respiration (Sayer et al., 2007). However, soil respiration is limited by temperature and moisture in neotropical humid forests and is found to decline with a

dry season decline in soil moisture (Chambers et al., 2004; Sotta et al., 2004; Zanchi et al., 2014). The integration and synthesis of the observed drought responses on the leaf, tree and ecosystem scale have not been carried out but are critical to highlight current knowledge gaps.

1.3 Can hydraulic behaviour explain differences in drought responses among species and studies?

Different tree species show markedly different responses to drought, both on the leaf level (Bonal et al., 2000a; Domingues et al., 2014) and the individual tree level (Esquivel-Muelbert et al., 2017a, 2017b; Phillips et al., 2009). The magnitude and direction of observed drought responses depend on the hydraulic behaviour of the particular species measured in that study (Bonal et al., 2000a; Fisher et al., 2006; Machado and Tyree, 1994). For example, species can adopt different drought avoidance and tolerance strategies (Volaire, 2018). Drought avoidance strategies aim to avoid a dangerous decline in ψ_l that could lead to significant xylem embolism and thus damage the hydraulic pathway. Maintaining a stable high ψ_l during drought can be achieved by strict stomatal control on transpiration (Huc et al., 1994; Machado and Tyree, 1994), increasing deep soil water uptake (Bonal et al., 2000b; Brum et al., 2019), maintaining a high plant internal water storage and conductance (Tyree et al., 2003; Wolfe, 2017) and through leaf shedding (Wolfe et al., 2016). Conversely, drought tolerance strategies imply that low leaf and xylem water potentials are tolerated without significant and irreversible embolism-induced losses of hydraulic function (Maréchaux et al., 2015; Markesteijn et al., 2011a; Tyree et al., 2003).

Tree hydraulic behavior is strongly dependent on the characteristics of the xylem sapwood (Janssen et al., 2020; Markesteijn et al., 2011b, 2011a; Meinzer et al., 2008b, 2008a; Wolfe, 2017). Species that do not avoid dehydration through stomatal closure are generally found to have xylem that is highly resistant to embolism, thus making them drought tolerant (Skelton et al., 2015; Vogt, 2001). Conversely, drought avoiding species are able to buffer declines in xylem water potential by using water that is stored in the sapwood (i.e. capacitance) and by strong stomatal control on transpiration (Borchert, 1994; Machado and Tyree, 1994; Meinzer et al., 2008b). In neotropical tree species, sapwood capacitance and conductivity decline while embolism resistance generally increases with increasing wood density (De Guzman et al., 2017; Janssen et al., 2020; Meinzer et al., 2008b; Santiago et al., 2018). This suggests that low wood density species can be considered drought avoiders while high wood density tree species are characterized as drought tolerant. Wood density is often not functionally related to the specific hydraulic properties (conductivity, capacitance and embolism resistance) that are driving hydraulic behavior (Janssen et al., 2020; Lachenbruch and Mcculloh, 2014). Nonetheless, wood density is an easily interpretable and widely available plant trait and therefore a useful proxy to compare different studies in which more specific hydraulic properties and traits were not measured. Therefore, we will use wood density as a proxy of hydraulic behavior in this meta-analysis and examine whether differences in study-averaged wood density explain the variability in observed leaf and tree scale responses to drought between different studies.

2 Methods

2.1 Data collection

The data collection focussed on published observations from the lowland humid forests of the neotropics, roughly between 20° South to 20° North (Figure 1, a). We searched the Web of Science for literature published between 1979 and 2019. This time frame matches the ERA5 reanalysis climate data (ECMWF, 2019) that was used to obtain harmonized meta-data for the retrieved literature. Publications were archived in a database if they contained one of the following variables: stomatal conductance, leaf photosynthesis, leaf water potential, stem sap flux density, tree daily transpiration, stem diameter increment, leaf flushing, leaf litterfall, ecosystem evapotranspiration, gross primary productivity, net primary productivity, ecosystem respiration and net ecosystem productivity. For studies that reported at least one of these variables, the observed values were stored in a database containing the reported value, the location and the month and year in which the measurement took place. For leaf scale measurements, all data included in the database were originally measured at midday (around 12:00 local time), except for pre-dawn leaf water potential which is measured just before sunrise (around 06:00 local time). Site measured soil matric potential was also included in the database. If possible, the leaf and tree scale variables of individual trees including genus and species name were stored in the database. Otherwise, site averages were used. Observations of ecosystem scale processes always consisted of site averages.

For every site in the database, the site biome was extracted from the *terrestrial ecoregions of the world map* from the World Wildlife Fund (Olson et al., 2001). Sites that were not located in the "Tropical and subtropical moist broadleaf forest" biome were omitted from the meta-analysis. Furthermore, the site elevation was extracted from the ALOS global 30m digital surface model (Tadono et al., 2016), which was aggregated to 1 km resolution using Google Earth Engine. All sites that were located at elevations higher than 1000 m a.s.l were regarded montane environments and were as such omitted from the meta-analysis. The final database used for the meta-analysis included observed drought responses from 145 published studies conducted across 232 sites in neotropical humid forests (Table S1 and S2).

Monthly averaged values of soil water content, air temperature and dewpoint air temperature at 2 meter above the surface were retrieved from the ECMWF ERA5 reanalysis product at 0.25 degree horizontal resolution (~28 km) (ECMWF, 2019). Values were retrieved for all the sites from January 1979 to August 2019. Monthly averaged air temperature and dewpoint temperature at four hourly averages (15:00 – 18:00 UTC) were used to retrieve monthly averaged midday (12:00 local time) temperature and dewpoint temperature in the four time zones covering the study area. These values were used to calculate monthly averaged midday vapor pressure deficit (VPD) following Buck (1981). The ERA5 retrieved monthly averaged midday VPD corresponded well with the monthly averaged midday VPD that was measured at 9 meteorological towers across the study area (Figure S1).

2.2 Data pre-processing and deriving additional variables

From the collected leaf, tree and ecosystem variables we derived additional variables of transpiration, productivity and water use efficiency. On the leaf level, we calculated the instantaneous intrinsic water use efficiency (iWUE, µmol mol^{-1}) at midday directly from the published data as:

$$iWUE = \frac{A}{g_s} \qquad (5)$$

where A is the midday leaf-area specific photosynthesis rate (µmol CO_2 m^{-2} s^{-1}) and g_s is the leaf-area specific stomatal conductance to water vapor (mol H_2O m^{-2} s^{-1}). On the tree scale, we calculated the instantaneous sapwood-area specific soil to leaf hydraulic conductance (kg dm^{-2} MPa^{-1} s^{-1}) following Love and Sperry (2018):

$$k_{sl} = \frac{J_{max}}{(\psi_{l\,pd} - \psi_{l\,md})} \qquad (6)$$

where J_{max} is the daily maximum sap flux density (kg dm^{-2} s^{-1}), $\psi_{l\,md}$ is the midday leaf water potential (MPa) and $\psi_{l\,pd}$ is the pre-dawn leaf water potential (MPa). Pre-dawn ψ_l is measured before the onset of leaf transpiration and considered a proxy of ψ_s in the root-zone. Therefore, the difference between midday ψ_l and pre-dawn ψ_l is regarded a proxy of the midday water potential gradient within the tree, from the root up to the canopy (Equation 3). Finally, we calculated leaf-area specific midday crown conductance (mol H_2O m^{-2} s^{-1}) following Meinzer et al. (1997):

$$G_c = \frac{J_{max} \left(\frac{A_s}{A_l}\right) P}{VPD} \qquad (7)$$

where J_{max} is the daily maximum sap flux density, but now in moles (mol m^{-2} s^{-1}), A_s/A_l is the sapwood area to leaf area ratio, P is atmospheric pressure, which was set to one standard atmosphere (101.325 kPa), and VPD is the monthly averaged midday vapor pressure deficit derived from ERA5 data.

On the ecosystem scale, the total net primary productivity (NPP) and above-ground NPP (ANPP) were calculated as the sum of stem growth and canopy growth, and for NPP also including root growth (sensu Doughty et al., 2015a; Hofhansl et al., 2014). Finally, the ecosystem water use efficiency was calculated as the ratio between gross primary productivity (GPP) and ecosystem evapotranspiration (sensu Yang et al., 2016).

To be able to compare drought responses of tree daily transpiration and ecosystem evapotranspiration with transpiration estimates based solely on observations performed on the leaf scale, we estimated potential midday leaf-area specific transpiration (mol m^{-2} s^{-1}) as:

$$E_{pot} = g_s \frac{VPD}{P} \qquad (8)$$

where g_s is the midday leaf-area specific stomatal conductance to water vapor and VPD is the monthly averaged midday VPD (kPa) derived from the ERA5 reanalysis data. In this estimation we use only the stomatal conductance and not the boundary layer conductance (Equation 1 & 2), which are often decoupled in large leaves and dense tropical forest canopies (Jarvis and Mcnaughton, 1986; De Kauwe et al., 2017; Meinzer et al., 1997). Using only stomatal conductance and not the total crown conductance likely causes a gross overestimation of absolute leaf transpiration and these estimates should never be used as a measure of actual leaf transpiration. Therefore, we only use potential leaf-scale transpiration in this meta-analysis to compare transpiration responses among different plant hydraulic strategies and omit this variable from the general analysis.

Many studies that measured sap flux density reported either the maximum daily sap flux density or the integrated daily sap flux density (daily transpiration). In 14 out of 34 studies that reported sap flux density results present in our database, only the maximum midday sap flux density values were reported but not the daily transpiration rates. As we find that maximum sap flux density and tree daily transpiration show a strong linear relationship for the studies included in our database (Figure S2), the sapwood-area specific daily transpiration for these studies was estimated as:

$$J_{daily} = 24 \left(\frac{J_{max}}{a} \right) \tag{9}$$

where J_{max} is the daily maximum sap flux density and a is a parameter fitted using a linear regression between maximum sap flux density and daily transpiration (Figure S2). Parameter a is essentially a factor describing the difference between J_{max} and daily average J per hour.

2.3 Dry season and drought definition

As the dry season progresses, soil moisture content, relative extractable soil water (REW) and soil matric potential decline as daily evapotranspiration surpasses precipitation (see e.g. Wright *et al.*, 1992; Nepstad, 2002). The occurrence of rain at the end of the dry season generally results in a rapid increase of soil matric potential and a relief of plant water stress (Fontes et al., 2018; Roberts et al., 1990; Tobin et al., 1999). Therefore, we define dry season months as months in which REW is reduced relative to the previous month (Figure 1 d). The REW is the amount of soil water available for plant uptake, which is often expressed as the volumetric soil moisture scaled between field capacity (REW = 1) and permanent wilting point (REW = 0). However, as there are insufficient measurements to construct reliable soil water retention curves across the study sites, we could not calculate REW. Instead, we estimated a pseudo REW as the normalized integrated soil moisture from ERA5, with 0 in the driest month and 1 in the wettest month of the entire timeseries (1979-2019) at that specific site (Figure 1, 2). Monthly integrated soil moisture over the entire soil profile was calculated as the weighted average of soil moisture content in all four soil layers (0 – 1.89 meter below the surface) provided in the ERA5 product. In neotropical humid forest, the bulk soil water is taken up from the first 1.3 meter of soil but this can extend up to 10-12 meters during drought (Brum et al., 2019; Davidson et al., 2011). To avoid a rapid oscillation of dry and wet season months over time due to small reductions or increases in REW, we labelled initially classified single dry season months in between two wet season months as wet season, and vice versa. We

find that, despite the uncertainties in ERA5 soil moisture data due to the underlying data assimilation and modelling, the ERA5 derived REW is able to accurately capture the seasonality of site measured soil matric potential ($R^2 = 0.5$, p < 0.001, Figure S3) and wet-dry season oscillations (Figure 1 d).

Dry season months where REW was lower than the 10% quantile of REW in all dry season months were labelled as episodic drought months (Figure 1 d). The 10% episodic drought threshold value was chosen as a reasonably strict episodic drought definition while still yielding a large enough sample size for the statistical analysis to differentiate between episodic drought and a regular dry season. We also performed a sensitivity analysis for this drought threshold by shifting the threshold to 15% of the driest dry season months (wide definition) and to 5% of the driest dry season months (narrow definition). We counted the number of episodic drought months recorded per year at each site (Figure 1 d) and in a regular 1° grid across the study area (Figure S4) to see how the occurrence of episodic droughts has changed over the past decades. We also used linear regression models to investigate correlations between ERA5 derived midday air temperature, midday VPD and number of episodic drought months per year (Table S3). The subdivision resulted in 2917 monthly observations in the wet season, 2968 in the dry season and 497 during episodic drought. We observe a significantly higher amount of episodic drought months in our meta-analysis than should be expected from the 10% quantile threshold used for delineating episodic droughts (i.e. 296.8). This can be explained by a high number of samples in recent studies that covered the 2015 ENSO drought (e.g. Doughty et al., 2017; Fontes et al., 2018; Maréchaux et al., 2018; Rifai et al., 2018; Santos et al., 2018).

In addition to monthly observations, stem growth data from the extensive forest inventory dataset of Brienen et al. (2015) was also included in the database. Because these data cover multiple months, we labelled census intervals that included at least three months of episodic drought as episodic drought and otherwise as dry season months for comparison. Finally, monthly values of the multivariate ENSO index for the period 1979-2019 were retrieved from the National Oceanic and Atmospheric Administration (http://www.esrl.noaa.gov/psd/enso/mei/). Strong ENSO years (1996-1997, 2009-2010, 2015-2016) are clearly visible as years with many recorded episodic drought months (Figure 1, Figure S4).

2.4 Meta-analysis

Quantitative drought responses of different plant physiological and ecosystem scale processes were synthesized using meta-analytical statistics. The log response ratio was used as a metric of drought effect size and converted back to percentage change for convenient interpretation. The log response ratio is the natural-log proportional difference between the means in a treatment and a control group (Hedges et al., 1999; Lajeunesse, 2011). In this analysis, we compared variables averaged over wet season months to variables averaged over dry season months, and in the second comparison the variables averaged over the dry season months with variables averaged over the episodic drought months (Figure 3). To be clear, we used only natural drought conditions in the meta-analysis and omitted all data that was acquired in artificial drought experiments. Measurements were always available in pairs or as repeated measurements (wet season-dry season, dry season-episodic drought), so that the

variance of the calculated response ratio has to be adjusted for by the Pearson product correlation coefficient between the measurement pairs (Lajeunesse, 2011). For individual tree measurements, which were available for stomatal conductance, photosynthesis, leaf water potential, tree transpiration and sometimes leaf flushing, the average, standard deviation and correlation coefficient were calculated from the pool of measured trees in each study. When site averages were used, which

290 was the case for all the other variables, the average and standard deviation calculated from the different measurement years were used. The log response ratio and sample variance of the variables in individual studies and sites were calculated using the *escalc* routine and the mean effect sizes and 95% confidence intervals in the *rma* routine, both available in the R package *metafor* (Viechtbauer, 2017).

295 To calculate the average wood density for each study, as a proxy of plant hydraulic behaviour, we created a separate dataset including for each study the genus and species names of the individual trees measured in the study. Preferably, the species-specific wood density was retrieved from the original source. However, if this was not possible, we retrieved wood density from a database of wood properties in neotropical tree taxa collated previously by us (Janssen et al., 2020) or from the global wood density database (Chave et al., 2009b; Zanne et al., 2009). Species-specific wood density was not available in 128 out

300 of 866 measured individuals. For these individuals, the genus averaged wood density was used instead. In neotropical tree taxa, 74% of interspecific variability in wood density can be explained by genus level variability in wood density (Chave et al., 2006). Therefore we consider genus average wood density as a suitable proxy for species level wood density in these cases. Furthermore, gap filling using genus averaged wood density prevents that missing values cause a large bias in the study averaged wood density in studies that measured relatively few species. Study averaged wood density was used in the *rma*

305 routine from the R package *metafor* (Viechtbauer, 2017) to test whether wood density was a significant moderator variable in the mixed-effect meta-regression model. This model also used inverse-variance weighting of the studies included in the model.

3 Results

3.1 Responses to seasonal drought

The meta-analysis shows that across the measured neotropical forest sites, a dry season decline in relative extractable water

310 (REW) is associated with a decline of soil matric potential in the topsoil (Figure 2 a, c, Figure S3). Furthermore, dry season months are characterised by a higher midday air temperature, lower relative humidity and therefore higher vapor pressure deficit (VPD) compared to wet season months (Figure 1 d, Figure 2 d). As a result of a decline in water supply from the soil and the increase of evaporative demand from the atmosphere, the meta-analysis indicates that across studies, pre-dawn and midday ψ_l both significantly decline from the wet to the dry season (Figure 2 a, Figure 3, a). Pre-dawn ψ_l declines from an

315 average -0.23 ±0.11 MPa in the wet season to -0.35 ±0.28 MPa in the dry season among studies and sites (Figure 2 a). Midday ψ_l declines from an average -0.89 ±0.34 MPa to -1.35 ±0.41 MPa from the wet to the dry season (Figure 2 a). Therefore, the average midday water potential gradient increases from 0.66 MPa in the wet season to 1.0 MPa in the dry season (Figure 3 b).

The dry season decline of ψ_l triggers progressive stomatal closure resulting in a decline of stomatal conductance and leaf photosynthesis of 42% and 25% from the wet to the dry season, respectively. As the decline in stomatal conductance outweighs the decline in leaf photosynthesis, intrinsic water use efficiency (iWUE) increases by 27% from the wet to the dry season (Figure 3, a). These results suggest that on the leaf scale, increased transpiration in the dry season is largely prevented by progressive stomatal closure, which is also contributing to a decline of leaf photosynthesis.

The meta-analysis shows that on the tree scale, there is a marginally significant increase of the water potential gradient while soil to leaf hydraulic conductance is not significantly reduced from the wet to the dry season (Figure 3 b). However, crown conductance is significantly reduced by 25% from the wet tot the dry season, suggesting that the increase of atmospheric VPD is offset by a decline in crown conductance that results in no significant change of tree daily transpiration from the wet to the dry season (Figure 3 b, Equation 1). The meta-analysis points to a distinct seasonality of alternating stem and canopy growth (Figure 3, b). The shedding of old and flushing of new leaves during the dry season cumulates into an average 30% higher leaf litterfall and 26% higher leaf flushing in the dry season, compared to the wet season. While canopy growth increases, average stem diameter growth declines by roughly the same magnitude (31%) from the wet to the dry season (Figure 3 b). These results suggest that generally, above-ground productivity alternates between stem and canopy growth from the wet to the dry season.

Despite no observed changes in tree daily transpiration, we observed a significant 9% increase of ecosystem evapotranspiration from the wet to the dry season (Figure 3 c). Furthermore, the meta-analysis also points to a 9% decline in gross primary productivity (GPP), resulting in a significant 19% reduction of ecosystem water-use efficiency from the wet to the dry season (Figure 3 c). Net primary productivity (NPP) declined by 10% from the wet to the dry season, but there was no significant change in above-ground net primary productivity (ANPP) from the wet to the dry season (Figure 3 c). This suggests that primarily root growth declines from the wet to the dry season, while increased canopy growth in the dry season is offset by a decline in stem growth (Figure 4 b). Considering the total ecosystem carbon budget, the decline of GPP is offset by a non-significant dry season decline of ecosystem respiration (R_{eco}) resulting in no significant change in net ecosystem productivity (NEP = GPP – R_{eco}) from the wet season to the dry season.

To test for the sensitivity of the observed responses to our episodic drought definition, we replicated the meta-analysis using a wide and a narrow drought definition, by setting the drought threshold at either 15% or 5% of the driest dry season months, respectively (Methods 2.3). For seasonal drought, changing the threshold did not significantly change the magnitude or direction of the observed responses (Figure S8 & S9). Slight changes in number of studies included in the analysis contributed to the increase of the water potential gradient from the wet to the dry season becoming not significant when using the wide drought definition (Figure S8 b) while the decline in soil to leaf hydraulic conductance from the wet to the dry season became marginally significant ($p < 0.05$) when using the narrow drought definition (Figure S9 b). These results suggest that the

observed responses to seasonal drought in this meta-analysis are robust, that is relatively insensitive to changes in the episodic drought threshold.

3.2 Responses to episodic drought

355 We found that on average, the number of months per year classified as episodic drought have been increasing since 1979, both in the studied plots (Figure 1 b) as well as across the entire study area (Figure S4). The number of episodic drought months per year increased significantly over time ($r = 0.62$, $p < 0.001$) and was positively correlated to annual averaged midday air temperature ($r = 0.82$, $p < 0.001$) and vapor pressure deficit ($r = 0.88$, $p < 0.001$) indicating both drying and warming over the past four decades (Figure S4, Table S3). Several previously described El Niño related drought events in 1983, 1987, 1997,
360 2010 and 2015 are superimposed on this trend and clearly visible as years with high midday air temperatures and VPD and relatively many episodic drought months per year (Figure 1 b, d, e, Figure S4).

Episodic droughts are associated with a higher VPD and a lower ψ_s compared to a regular dry season (Figure 1 d, Figure 2 a, d). Consequently, the pre-dawn ψ_l is on average 0.32 MPa lower (-0.67 ±0.52 MPa) during episodic drought compared to an
365 average dry season (-0.35 ±0.28 MPa) (Figure 2 a, Figure 3 a). Midday ψ_l declines from -1.35 ±0.41 MPa in the dry season to -1.8 ±0.48 MPa during episodic drought, increasing the average water potential gradient by 0.13 MPa across all measured trees. However, the meta-analysis indicates that this increase is not significant as there is a large variability in the water potential gradient response to episodic drought (Figure 3 b). The decline of midday ψ_l in response to episodic drought is related to a 49% reduction of stomatal conductance and 27% reduction in leaf photosynthesis compared to a regular dry season
370 (Figure 3 a). Similar to seasonal drought, we observe a small increase of iWUE in response to episodic drought but this response is not significant (Figure 4 a).

On the tree scale, there is no significant change in the water potential gradient during episodic drought compared to a regular dry season and also the substantial average decline of 53% in soil to leaf hydraulic conductance during episodic drought
375 compared to a regular dry season is not significant (Figure 3 b). Nonetheless, we do observe a significant decline of 36% in crown conductance and a 18% decline of tree daily transpiration in response to episodic drought (Figure 3 b). Furthermore, stem diameter growth is reduced by an average 6% during episodic drought compared to a regular dry season while leaf flushing and litter fall are not significantly different (Figure 4 d).

380 On the ecosystem scale, despite the decline in tree transpiration, the meta-analysis suggests that evapotranspiration during episodic drought is not significantly different to the evapotranspiration in the dry season (*Random-effects model, p = 0.63, n = 5*). Furthermore, despite declines in stem growth and leaf photosynthesis during episodic drought (Figure 3 a, b) there are no significant differences in GPP, NPP, ANPP and ecosystem water use efficiency between episodic drought and a regular dry season (Figure 3 c). However, we do observe a significant 9% decline in ecosystem respiration that is driving a 24% increase

of net ecosystem productivity in response to episodic drought (Figure 3 c). These results suggest that ecosystem productivity is relatively tolerant to episodic drought while reduced respiration contributes to a net increase of ecosystem carbon uptake during episodic drought compared to a regular dry season.

The sensitivity analysis showed that some episodic drought responses are sensitive to changes in the episodic drought threshold, especially on the leaf scale (Figure S8 & S9). When using both the narrow and wide episodic drought definition, the decline in leaf photosynthesis in response to episodic drought became not significantly different from a regular dry season anymore (Figure S8 a, S9 a). For the narrow definition this is mainly the result of using only half the number of studies compared to the baseline analysis, reducing the statistical power of the test. In the wide definition analysis, the effect size, or the difference between the episodic drought and a regular dry season month, becomes smaller. Choosing an arbitrary episodic drought threshold to compare a regular dry season with an episodic drought will always result in uncertainties of the observed responses. However, after testing the sensitivity of the episodic drought threshold we conclude that most of the observed responses to seasonal and episodic drought are robust, while highlighting the importance of choosing an episodic drought threshold that is strict enough (i.e. only includes exceptionally dry conditions) while it still yields a large enough sample size for the statistical analysis to differentiate.

3.3 Relationships between study-averaged wood density and drought responses

The meta-analysis revealed that on average, stomatal conductance and leaf photosynthesis are downregulated as pre-dawn and midday ψ_l decline during seasonal and episodic drought. Furthermore, we find that between-study variation in the stomatal conductance, potential leaf transpiration and leaf photosynthesis response to seasonal and episodic drought correlates with differences in study-averaged wood density. Generally, studies that measured mainly low wood density tree species showed a stronger response of stomatal conductance and potential leaf transpiration to seasonal and episodic drought compared to studies that measured mainly high wood density species (Figure 4 a, b). Also the magnitude of a decline in leaf photosynthesis in response to seasonal drought decreased with increasing wood density (Figure 4 c). However, this relationship was not visible in response to episodic drought (Figure 4 c). There was also no significant effect of wood density on the response of midday ψ_l to seasonal or episodic drought (Figure 4 d) but there was a significant relationship between the episodic drought response of pre-dawn ψ_l and study averaged wood density ($R^2 = 0.76$, $p < 0.05$, not shown). Generally, studies that measured high wood density species showed a stronger decline of pre-dawn ψ_l in response to episodic drought, compared to studies that measured low wood density species. These results suggest that low wood density species are better able to maintain a high pre-dawn ψ_l during episodic drought, possibly because of strong stomatal control on transpiration (Figure 4 a, b), higher sapwood capacitance, or because of deep soil water accessibility that enables recharging of tissue water at night.

For similar reasons, we find that the response of midday ψ_l to a decline in pre-dawn ψ_l is also strongly dependent on study-averaged wood density (Figure S5). Tree species from studies with a high average wood density (> 0.7 g cm^{-3}) showed a strong

reduction in midday ψ_l and increase the water potential gradient in response to a decline in pre-dawn ψ_l. On the other hand, tree species in studies with a low average wood density species (< 0.5 g cm^{-3}) show a non-significant decline of midday ψ_l in response to a decline in pre-dawn ψ_l. Studies with intermediate average wood density (0.5-0.7 g cm^{-3}) show a decline of midday ψ_l parallel to a decline in pre-dawn ψ_l (slope ~1) (Figure S2). Related to these results we found that the stomatal response to atmospheric VPD also depends on study-averaged wood density, with low wood density species showing strong stomatal downregulation in response to increased atmospheric VPD, while no stomatal downregulation is observed in high wood density species (Figure S6). These results imply that low wood density species prevent a midday drop in ψ_l during seasonal and episodic drought by downregulating stomatal conductance, potential leaf transpiration and photosynthesis in response to elevated midday VPD, while high wood density tree species keep a more variable ψ_l and have no strong stomatal control on potential leaf transpiration.

The dry season responses of the two tree-scale variables for which enough species-specific data was available, tree daily transpiration and leaf flushing, also showed significant relationships with study-averaged wood density (Figure 4 e, f). The relationship between study-averaged wood density and the magnitude of the seasonal drought response of tree daily transpiration was similar in terms of magnitude and direction as the relationship between wood density and the potential leaf transpiration response (Figure 4 b, Figure 4 e). Roughly half of the studies that measured mainly low wood density species showed a dry season decline in tree transpiration. The other half of the studies that measured mainly high wood density species showed a dry season increase of tree transpiration (Figure 4 e). Similarly, dry season leaf flushing is found to be more pronounced in high wood density species compared to low wood density species that actually show on average a decline of leaf flushing in the dry season (Figure 4, f). Finally we find that study-averaged stomatal conductance, leaf photosynthesis, midday ψ_l, tree daily transpiration, soil to leaf hydraulic conductance and crown conductance all significantly decline with increasing study-averaged wood density (Figure S7). These results suggest that low wood density species, compared to high wood density species, are characterized by efficient water transport, high stomatal conductance and leaf photosynthesis during the wet season but also show a strong decline of stomatal conductance, transpiration and photosynthesis in response to drought.

4 Discussion

4.1 How do leaf, tree and ecosystem scale processes respond to seasonal drought?

Stomatal behaviour, changes in soil to leaf hydraulic conductance and differences in hydraulic architecture determine the hydraulic response to seasonal drought in neotropical trees, driving tree transpiration and ecosystem evapotranspiration (Figure 2 & 3). The downregulation of stomatal conductance and canopy conductance in the dry season is a widely observed hydraulic response to a decline in leaf and xylem water potential (Fisher et al., 2006; Machado and Tyree, 1994; Williams et al., 1998). However, progressive stomatal closure, the decline in hydraulic conductance and crown conductance are offset by a higher

midday VPD and an increase of the water potential gradient (midday ψ_l - pre-dawn ψ_l) in the dry season, resulting in no observed change in tree daily transpiration from the wet to the dry season across studies (Figure 3). The decline of soil to leaf hydraulic conductance in the dry season is the result of embolism formation in the xylem vessels that reduces xylem hydraulic conductance (Bonal et al., 2000a; Fontes et al., 2018; Machado and Tyree, 1994; Meinzer et al., 2008b). Our data did not allow us to disentangle whether dry season transpiration is mainly constrained by a decline in stomatal conductance or a decline in soil to leaf hydraulic conductance. However, the decline of hydraulic conductance and stomatal conductance with decreasing xylem water potential are strikingly similar (Brodribb et al., 2003) suggesting that xylem hydraulic vulnerability and stomatal sensitivity are strongly coordinated (Fontes et al., 2018; Maréchaux et al., 2018; Meinzer et al., 2008b).

The meta-analysis suggests that the dry season downregulation of stomatal conductance is accompanied by a smaller but significant decline in leaf photosynthesis (Figure 3 a). Therefore, the leaf-scale intrinsic water use efficiency (iWUE) increases on average from the wet to the dry season (Figure 3 a). This increase of iWUE in the dry season was also found in earlier site-specific studies (Bonal et al., 2000a; Hogan et al., 1995; Santos et al., 2018). However, as gross primary productivity (GPP) declines and evapotranspiration increases, we observe a decline of ecosystem water use efficiency from the wet to the dry season (Figure 3 c). Therefore, our results suggests that despite leaf level iWUE increases from the wet to the dry season, neotropical forests actually become less water efficient in the dry season. This is in agreement with a global synthesis of eddy-covariance measurements that showed that humid tropical forests show a decline of ecosystem water use efficiency in response to drought (Yang et al., 2018a).

The meta-analysis results show that across neotropical forests, net primary productivity (NPP) declines while above-ground NPP (ANPP) does not change from the wet to the dry season (Figure 3 c). This suggests that the decline in total NPP is primarily the result of a decline in root growth in the dry season. We confirm earlier findings that root growth declines with a decline in soil moisture in the dry season (Girardin et al., 2016; Metcalfe et al., 2008). Furthermore, we find that above-ground growth is shifted from the stem in the wet season to the canopy in the dry season (Figure 3 b) without changes in overall above-ground growth. Finally, the meta-analysis shows that the dry season decline of GPP is offset by the decline of ecosystem respiration, resulting in no significant change in net ecosystem productivity from the wet to the dry season (Figure 3 c). The dry season decline of ecosystem respiration is likely driven by a decline of heterotrophic respiration from the soil and litter layer as soil and litter respiration is found to be strongly dependent on the availability of moisture in neotropical forests (Chambers et al., 2004; Sotta et al., 2004; Zanchi et al., 2014).

4.2 How do leaf, tree and ecosystem scale processes respond to episodic drought?

Episodic droughts seem to have become more common in South and Central America recently. Previously classified as once in a century episodic droughts are now occurring roughly every five years (Aragão et al., 2007; Coelho et al., 2012; Erfanian et al., 2017; Marengo et al., 2008, 2011; Panisset et al., 2017). Furthermore, ENSO extremes that are clearly linked to major

droughts in neotropical forests (Figure 1, Figure S4) have been intensifying in the 20th and 21st century (Grothe et al., 2019). Following our definition of episodic drought, we observe a significant increase of the number of episodic drought months per year since 1979, both across the 232 neotropical forest sites (Figure 1 b) as well as across the entire humid neotropical forest biome (Figure S4). Although this drying trend might be the result of an underlying bias in the ERA5 reanalysis product, the result is in agreement with the analysis of alternative datasets indicating that dry seasons in Amazonia have been becoming dryer since 1979 (Fu et al., 2013). The mechanisms driving this dry season drying are uncertain but have been attributed to changes in global atmospheric circulation (Fu et al., 2013) and more regionally to deforestation (Costa and Pires, 2010; Debortoli et al., 2017). We also find that midday air temperature and VPD have been increasing over the same period (Figure S4), suggesting that episodic drought have not only become more frequent but also hotter since 1979. In this meta-analysis, we were able to use leaf, tree and ecosystem scale data from five major episodic drought years, namely from 1987, 1997, 2005, 2010 and 2015 (Figure 1).

Episodic droughts reduce the supply of water from the soil and increase the evaporative demand of the atmosphere beyond values that are observed in a regular dry season (Figure 2) (see also Jiménez-Muñoz et al., 2016; Lee et al., 2013; Panisset et al., 2017). We find that both stomatal conductance and photosynthesis are reduced during episodic drought compared to a regular dry season (Figure 3 a). This suggests that the physiological responses to episodic drought on the leaf level are, in terms of direction and magnitude, a continuation of the seasonal drought response. Stomatal limitations may explain the observed decline of leaf photosynthesis in response to episodic drought, as changes in nutrient or chlorophyll concentrations were not reported for the 2015 drought in the central Amazon (Santos et al., 2018). Alternatively, reductions in carboxylation capacity and mesophyll conductance in response to leaf desiccation or high leaf temperatures could cause a more permanent reduction of photosynthesis during episodic drought (Dewar et al., 2018; Doughty, 2011; Felsemburgh, 2009; Lloyd and Farquhar, 2008; Zhou et al., 2013). The average midday ψ_l observed during episodic drought (-1.8 MPa) induces leaf turgor loss in many tropical rainforest trees (Maréchaux et al., 2015). The importance of tissue desiccation and heat-induced damage to the photosynthetic machinery is presently not known but could become increasingly important in the tropical carbon cycle in a warmer climate.

The meta-analysis results suggests that stem growth is significantly reduced during episodic drought while leaf litter fall and leaf flushing do not show a consistent positive or negative change (Figure 3 b). The decline of stem growth during episodic drought is widely observed across tropical humid forests and has been linked to a temporary decline in tropical forest carbon sink (Brienen et al., 2015; Clark et al., 2003, 2018; Feldpausch et al., 2016; Rifai et al., 2018). However, declines in stem growth are not always obvious (Doughty et al., 2014, 2015; Phillips et al., 2009) and are at some sites compensated for by an increase in canopy growth or root growth (Doughty et al., 2015; Hofhansl et al., 2014) resulting in no observed net change in NPP or ANPP during episodic drought (Figure 3 c). These results suggest that despite significant reductions in leaf photosynthesis during episodic drought, overall tree growth is not limited by carbohydrate availability (carbon starvation)

(Mcdowell et al., 2008; Sala et al., 2012). Evidence from neotropical humid forests suggests that leaf and wood tissue concentrations of non-structural carbohydrates (NSC's) are kept relatively constant during seasonal and severe episodic drought (Dickman et al., 2019; Würth et al., 2005). This implies that temporary reductions in photosynthesis are not sufficient to limit actual tree growth during drought (Würth et al., 2005). The significant decline in stem growth in response to episodic drought is more likely driven by cell turgor loss in the vascular cambium as a result of tissue desiccation, which limits cell formation and thus the formation of new tissue in the stem (Körner and Basel, 2013; Krepkowski et al., 2011; Muller et al., 2011). It is essential to understand which mechanisms, turgor mediated, carbon mediated, or a combination of both, are driving drought-induced declines in tree growth, as they can operate on different time scales and can have different sensitivities to drought.

4.3 What are the differences between seasonal and episodic drought?

We find that the responses of stomatal conductance, leaf photosynthesis, midday and pre-dawn ψ_l to episodic drought are basically a continuation of the same leaf physiological responses observed during seasonal drought (Figure 2 & 3). However, unlike seasonal drought, the decline in crown conductance outweighs the increase of atmospheric VPD during episodic drought, effectively reducing tree daily transpiration (Figure 4 a, b, Equation 1). Our results are in agreement with site-specific observations that tree daily transpiration is reduced through a combination of stomatal downregulation and a loss of soil to leaf hydraulic conductance, both in response to episodic drought (Fontes et al., 2018) and multi-year drought (Fisher et al., 2006). Unlike the rapid recovery of stomatal conductance, soil to leaf hydraulic conductance has been observed not to recover fully after episodic drought (Fontes et al., 2018) imposing a legacy effect on transpiration in the first months following episodic drought. Furthermore, the loss of hydraulic conductance might be considered an early warning signal for embolism-induced drought mortality (Rowland et al., 2015b) following episodic drought (Feldpausch et al., 2016; Phillips et al., 2009). The decline of tree transpiration in response to episodic drought likely results in the decline of the surface latent heat flux and increase of the surface sensible heat flux, causing a further drying and warming of the atmosphere (Harper et al., 2014).

Contrary to seasonal drought, we observe no increase in leaf flushing and litterfall and no significant declines in NPP and GPP during episodic drought. One explanation for this apparent discrepancy is that leaf flushing, litterfall, NPP and GPP operate on seasonal timescales and are strongly dependent on tree phenology. Most neotropical tree species shed old and flush new leaves during the dry season as their leaf phenology is synchronized to maximum daily insolation (Borchert et al., 2015; Bradley et al., 2011; Brando et al., 2010; Graham et al., 2003; Wagner et al., 2016; Wright and van Schaik, 1994). This results in an initial decline followed by a progressive increase of photosynthetic capacity on the ecosystem scale in the late dry season as leaves mature (Albert et al., 2018; Doughty and Goulden, 2009b; Wu et al., 2016). Leaf flush and maturation, and with it the increase of leaf photosynthetic capacity, drive a progressive increase of GPP during the dry season in humid neotropical forests (Albert et al., 2018; Araújo et al., 2016; Doughty and Goulden, 2009b; Hutyra et al., 2007; Restrepo-Coupe et al., 2013). Episodic droughts by our definition always occur at the end of the dry season, when REW is lowest (Figure 1).

Therefore, the peaks in litter fall and leaf flush that generally occur in the first half of the dry season, have already occurred
550   before the episodic drought starts and therefore GPP is relatively high. We hypothesize that the seasonal timescales of tree phenology and ecosystem productivity could be counteracting the potential negative effects of short episodic droughts on GPP, which were therefore not observed in the meta-analysis.

4.4 How do we scale from the leaf to the ecosystem?

Our meta-analysis indicates a general tendency of seasonal and episodic drought responses becoming smaller and not
555   significant when going from the leaf and tree scale to the ecosystem scale. Regarding transpiration, we observed sustained tree daily transpiration in the dry season and a decline of tree daily transpiration in response to episodic drought (Figure 3 b). In contrast, ecosystem evapotranspiration increases significantly in the dry season and does not significantly change during episodic drought (Figure 3 c). This discrepancy is not logically explained by an increased contribution of evaporation from the soil and canopy to evapotranspiration, as both soil and canopy evaporation are expected to be lower in the dry season and
560   during episodic drought compared to the wet season (Shuttleworth, 1988). A more likely explanation is that the leaf and tree-scale data used in our meta-analysis are biased towards fast-growing pioneer tree species with low wood density that are growing in upper canopy positions (e.g. Dünisch and Morais, 2002; Huc et al., 1994; Kunert et al., 2010; Machado and Tyree, 1994).

565   Stomatal control on transpiration is stronger in low wood density compared to high wood density tree species (Figure 4, Figure S6). Furthermore, sun-exposed trees in upper canopy positions experience a higher evaporative demand from the atmosphere, resulting in a more pronounced downregulation of stomatal conductance and photosynthesis in response to seasonal and episodic drought compared to understory trees (Domingues et al., 2014; Fisher et al., 2006; Santos et al., 2018). This sample bias in the meta-analysis might also explain why ecosystem scale responses of carbon exchange to drought seem to contradict
570   the observations on the leaf and tree scale. The decline of leaf photosynthesis is more than twice the magnitude of the decline in GPP during seasonal drought, while in response to episodic drought there is not even a decline in GPP detected (Figure 3). This meta-analysis result is confirmed by unexpected results from previous studies that found that GPP and NPP are not reduced during episodic drought despite significant declines of leaf photosynthesis (Bonal et al., 2008; Doughty et al., 2014, 2015).

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Another explanations for the apparent contradiction between leaf, tree and ecosystem scale responses to episodic drought is the limited timescale on which we analysed ecosystem drought responses. The temporal scale of some tree and ecosystem scale responses to episodic drought might extend far beyond the actual drought (e.g. Gonçalves et al., 2020; Hofhansl et al., 2014). For example, episodic drought events have been found to elevate tree mortality rates across neotropical forests (Condit
580   et al., 1995; Feldpausch et al., 2016; Phillips et al., 2009; Williamson et al., 2000). Tree mortality can significantly impact ecosystem productivity and transpiration, carbon storage and canopy structure, impacting the understory light environment

and microclimate for many years (da Costa et al., 2018; Leitold et al., 2018; Rice et al., 2004, 2008; Rowland et al., 2018; Saatchi et al., 2013; Yang et al., 2018a). Furthermore, extensive leaf flushing in the first months after an episodic drought have been reported (Doughty et al., 2014, 2015; Gonçalves et al., 2020; Hofhansl et al., 2014) contributing to ANPP exceeding pre-drought values in the years directly following episodic drought (Doughty et al., 2014, 2015; Hofhansl et al., 2014). These legacy effects of drought are not captured by or meta-analysis, which is a limitation of the method used. Therefore, we were unable to grasp the complete, or final extent of the tree and ecosystem scale responses to episodic drought.

4.5 How is wood density related to leaf and tree scale responses to drought?

The meta-analysis shows that the magnitude and direction of the stomatal conductance, leaf photosynthesis, potential leaf transpiration, tree daily transpiration and leaf flushing response to seasonal drought is strongly related to the wood density of trees measured in a particular study (Figure 4). The same relationship was observed for stomatal conductance and potential leaf transpiration in response to episodic drought (Figure 4). Generally, we find that studies that measured tree species with a relatively low wood density showed a drought avoiding response, including strong stomatal control on transpiration and no dry season leaf flushing (Figure 4). Conversely, studies that measured tree species with a relatively high wood density showed no stomatal downregulation, increased leaf and tree-scale transpiration and increased leaf flushing in the dry season (Figure 4). As a result, high wood density trees show a stronger desiccation of the leaves and stem during drought and a lower midday leaf and xylem water potential (Figure S5 & S7) (Borchert, 1994; De Guzman et al., 2017; Meinzer et al., 2008b; Sterck et al., 2014). Wood density appears a good proxy of hydraulic behaviour and could well be used to predict responses of stomatal conductance, transpiration and leaf flushing to seasonal and episodic drought (see e.g. Christoffersen et al., 2016).

Differences in wood density among tree species have been widely studied and are linked to differences in plant hydraulic architecture and hydraulic properties such as hydraulic conductance, sapwood capacitance and embolism resistance (Baas et al., 2004; Chave et al., 2009a; Janssen et al., 2020; Poorter et al., 2010). The use of wood density as a proxy of more fundamental hydraulic properties has been criticized as it often lacks a functional basis (Lachenbruch and Mcculloh, 2014; Patiño et al., 2012). Sapwood capacitance, the amount of water released from the xylem under a certain pressure, is arguably the only hydraulic property that is functionally related to wood density, as the amount of space available for water storage in the wood scales inversely with wood density (Janssen et al., 2020; Meinzer et al., 2008b; Poorter, 2008; Pratt and Jacobsen, 2017; Ziemińska et al., 2019). Sapwood capacitance is positively related to maximum stomatal conductance, leaf photosynthesis, tree daily transpiration, soil to leaf hydraulic conductance and midday ψ_l (Meinzer et al., 2003; Oliva Carrasco et al., 2015; Santiago et al., 2004). We show that these relationships hold when relating not species but study-averaged wood density, as a proxy of sapwood capacitance, to study-averaged stomatal conductance, leaf photosynthesis, tree daily transpiration, midday ψ_l, crown conductance and soil to leaf hydraulic conductance (Figure S7). Our results suggest that wood density, via sapwood capacitance, is largely driving the magnitude of the stomatal and transpiration response to seasonal and episodic drought in neotropical trees.

615   The difference in hydraulic behaviour between low and high wood density tree species is confirmed by the observation that the decline of stomatal conductance with atmospheric VPD and the slope of the relationship between midday ψ_l and pre-dawn ψ_l are strongly dependent on wood density (Figure S5 & S6). We find that low wood density trees with high sapwood capacitance show a relatively high maximum soil to leaf hydraulic conductance as stored water is used for transpiration (Figure

620   S7) while stomatal conductance is downregulated with increasing VPD in the dry season to avoid dehydration (Figure S6) (Goldstein et al., 1998; Meinzer et al., 2004, 2008b). Conversely, in high wood density trees, transpiration is primarily constrained by the relatively low soil to leaf hydraulic conductance all year around and stomatal downregulation plays a minor role. High wood density trees maintain stomatal conductance ($0.07 - 0.14$ mol m^{-2} s^{-1}) even during severe episodic drought (Alexandre, 1991; Bonal et al., 2000a; Roberts et al., 1990; Santos et al., 2018; Stahl et al., 2013b). This implies that

625   transpiration has to increase during seasonal and episodic drought in high wood density trees, resulting in a significant decline of midday ψ_l (Figure 4, Figure S5) (Alexandre, 1991; Bonal et al., 2000a; Brum et al., 2019; Domingues et al., 2014). The observed insensitivity of stomatal conductance to VPD in high wood density trees has been reported previously for lowland rainforest species (Bonal et al., 2000a; Domingues et al., 2014; Granier et al., 1992; Huc et al., 1994). Stomatal insensitivity to VPD is a possible adaptation to surviving in a humid and deeply shaded understory, as the CO_2 concentration inside the leaf

630   is kept high to maximize photosynthesis during brief moments of high irradiance, known as sun flecks (Domingues et al., 2014; Pons et al., 2005; Tinoco-Ojanguren and Pearcy, 1992).

The capability to maintain stomatal conductance and transpiration during short episodic droughts has been explained by the uptake of deep soil moisture using tap roots (Bonal et al., 2000a; Brum et al., 2019; Meinzer et al., 1999; Nepstad et al., 1994;

635   Stahl et al., 2013a, 2013b). Soil water at a depth of up to 18 meters was found to be accessible for trees at Tapajós in the eastern Amazon (Davidson et al., 2011), enabling trees to maintain a favourable water status during short dry periods. This also becomes clear from the relatively high average pre-dawn ψ_l during episodic drought (-0.67 MPa), compared to tree species of tropical dry forest where pre-dawn ψ_l can approach -2.5 MPa in a regular dry season, inducing leaf wilting and high mortality rates in tree seedlings (Sobrado, 1986; Veenendaal et al., 1996). Soil depth, root functioning and differences in root architecture

640   are believed to be crucial regulators during drought (Brum et al., 2019; Meinzer et al., 1999; Stahl et al., 2013a), but lack of data in neotropical forests prevented us from including these traits in our meta-analysis.

Deep soil moisture uptake is not always sufficient to maintain a favourable water status within the tree as drought-induced tree mortality events have been widely observed across the neotropics (Condit et al., 1995; Feldpausch et al., 2016; Phillips et al.,

645   2009; Williamson et al., 2000), likely resulting from hydraulic failure (Rowland et al., 2015b). The effect of an increased evaporative demand during drought should not be overlooked, as a high VPD can trigger xylem embolism in trees even when soil water is still easily accessed (Fontes et al., 2018; Phillips et al., 2001). Our results point to the lack of drought avoidance in high wood density tree species as stomatal conductance and transpiration are sustained under high evaporative demand,

resulting in a strong decline of xylem and leaf water potential during drought (Figure 4, Figure S5 & S6). However, many high wood density tree species in humid neotropical forests have evolved in permanently wet environments and are not always tolerant against xylem embolism (Janssen et al., 2020; Powell et al., 2017; Santiago et al., 2018). The combination of relatively low sapwood capacitance, limited stomatal control on transpiration and limited embolism resistance can amount to high drought-induced mortality rates in some of these high wood density tree taxa (Janssen et al., 2020). This highlights the fact that a lack of properties contributing to drought avoidance in a particular individual or species are not always compensated for by a high drought tolerance, making this individual or species highly vulnerable to drought-induced mortality.

5 Conclusions

In this study, we performed a meta-analysis that provides a quantitative overview of leaf, tree and ecosystem responses to seasonal and episodic drought in neotropical humid forest. We find that the observed leaf-scale responses to episodic drought are a continuation of the responses observed during seasonal drought: reductions in leaf water potential, stomatal conductance and photosynthesis. The observed dry season decline in stem growth and increases of leaf flushing and litter fall seem to be unrelated to water stress. Rather, the seasonal oscillation of growth allocation between stem and canopy seems to be driven by tree phenology which is synchronised to maximum incoming solar radiation in the dry season. Drought responses related to stomatal and hydraulic conductance, transpiration and photosynthesis are adequately captured by our approach because these responses occur on relatively short time-scales of hours and weeks with the opening and closure of leaf stomates, the occurrence of xylem embolism and the flushing of new leaves. However, tree and ecosystem scale responses related to productivity and growth allocation are also dependent on carbohydrate status which operates on seasonal to multi-annual timescales. The meta-analysis confirms that the variability and magnitude of drought responses decline when going from the individual leaf to the ecosystem level in highly diverse tropical forests. Biodiversity driven dynamics at the community level, such as niche partitioning, likely contribute to ecosystem resistance and resilience in response to episodic drought. Finally, we found that wood density, via its direct relationship with sapwood capacitance, acts as a good proxy of hydraulic behaviour and largely explains the magnitude of stomatal and transpiration responses to seasonal and episodic drought.

Data availability

The data compiled for this study and used in the meta-analysis is available at https://hdl.handle.net/10411/41KALW

Author contribution

T.J., S.L. and H.D. designed the research, T.J., K.F., S.L., K.N. and H.D. coordinated the writing and contributed ideas, T.J. compiled the database and analysed the data, K.F., S.L., K.N. and H.D. assisted with writing the final manuscript

Competing interests

The authors declare that they have no conflict of interest

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Figures
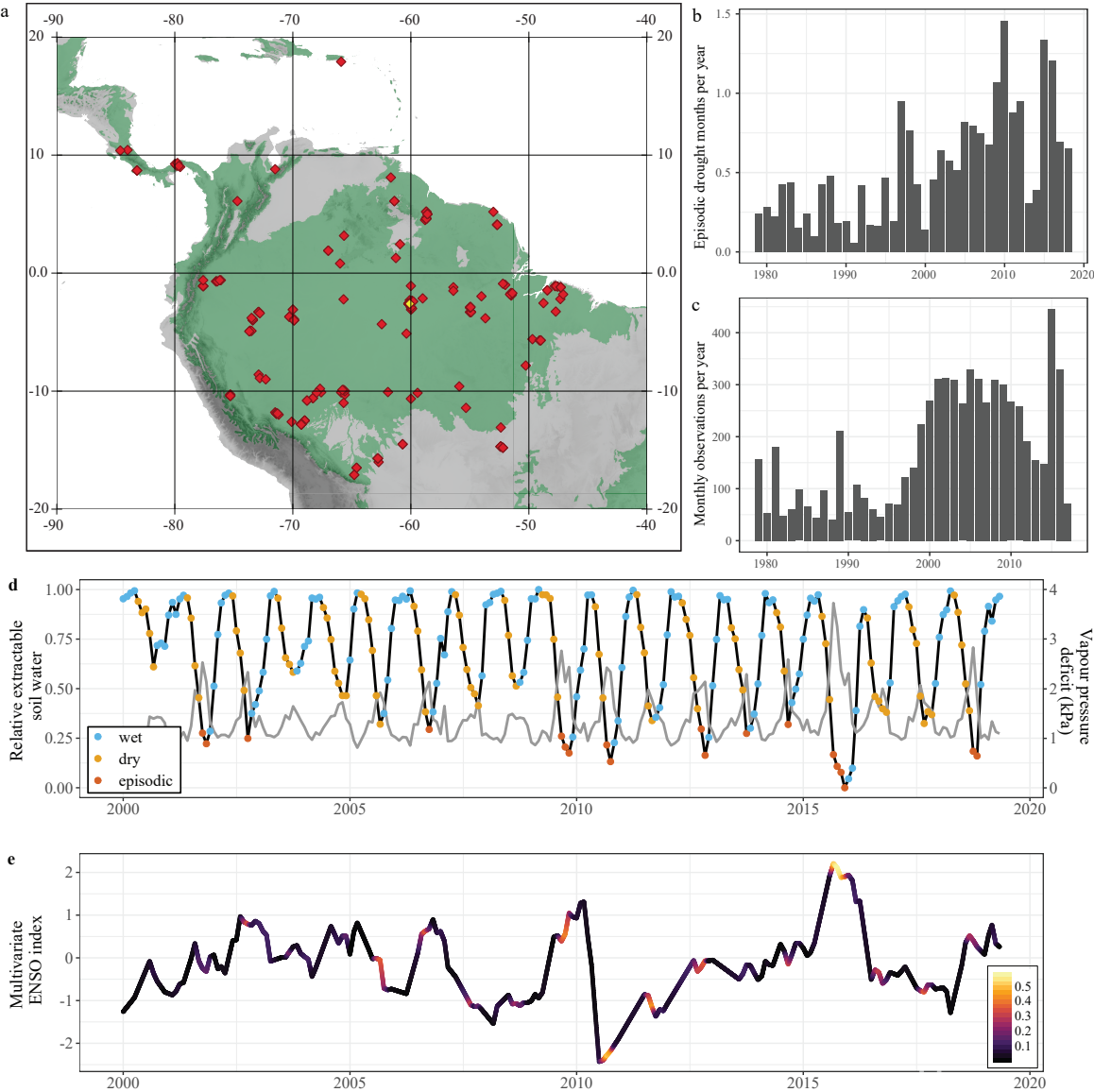
Figure 1: Summary of the database. Site locations (a), average number of episodic drought months per year (b) and number of monthly observations in the database per year (c). The map shows the locations of the 229 neotropical forest sites from which data was used in this meta-analysis. In green, the distribution of tropical and subtropical moist broadleaf forest from the terrestrial ecoregions of the world map (Olson et al. 2001). The average number of episodic drought months per year (b) was calculated as the average number of months classified as episodic drought per year recorded at all sites, independent of whether we have field data for these months. Below, a monthly time-series of relative extractable water (light grey) and vapour pressure deficit (dark grey) for the K34 site in the central Amazon (d), indicated in yellow on the map (a). The coloured dots indicate whether that specific month was classified as a wet season, dry season or episodic drought month. (e) shows a timeseries of the multivariate ENSO index with positive values indicating El Niño (dry) conditions and negative values La Niña (wet) conditions. The colouring of the ENSO index represent the number of episodic drought months recorded per month across the sites in the database, ranging from 0 (no droughts recorded) to 0.58 (episodic drought in 58% of the plots).

1250
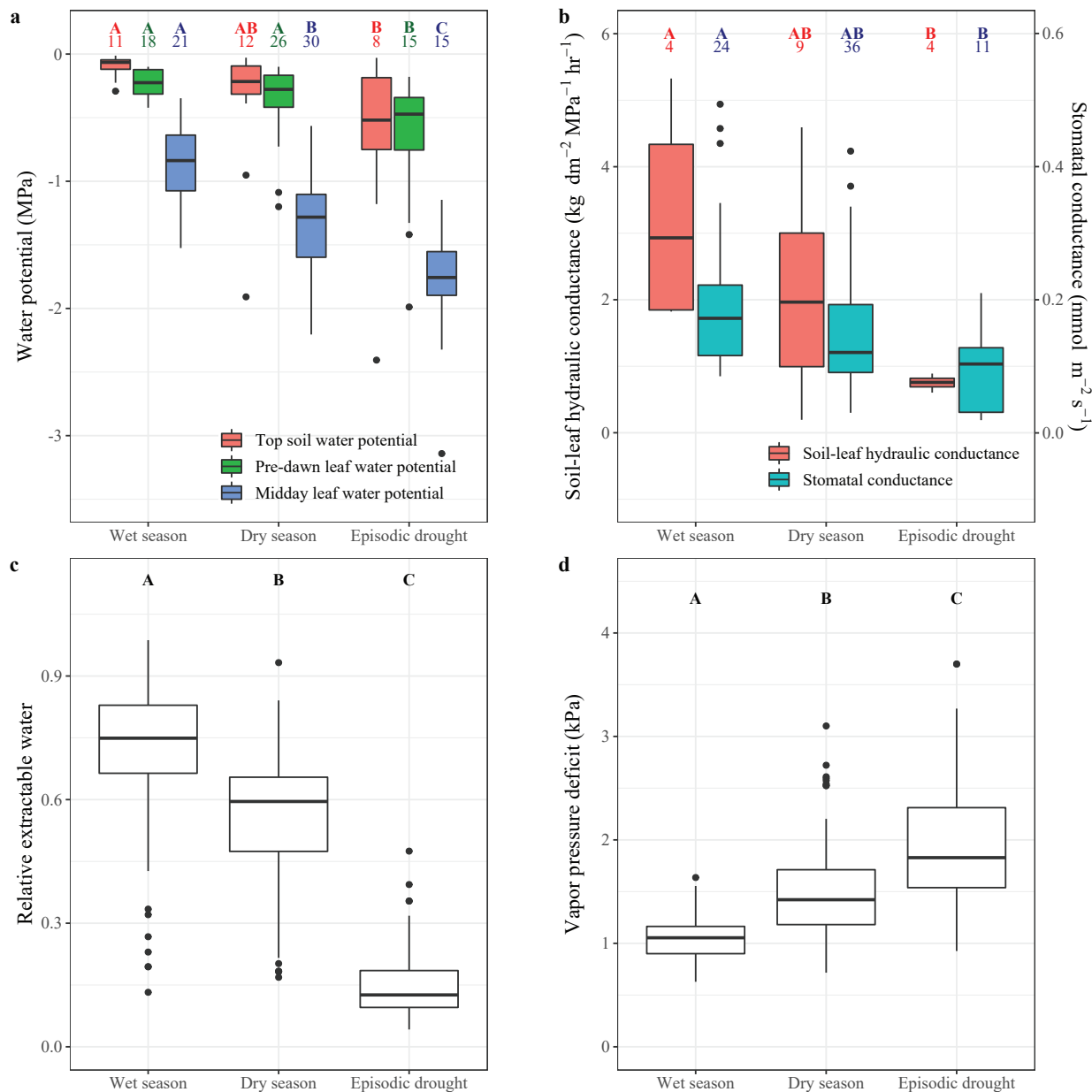
Figure 2: Plant hydraulic status, plant hydraulic conductance, stomatal conductance and environmental drivers in the wet season, dry season and during episodic drought. The boxplots show the median value, interquartile ranges (boxes), the whiskers show the range between minimum and maximum value and, if present, outliers are indicates as single dots. Soil matric potential, pre-dawn leaf water potential, midday leaf water potential (a), soil to leaf hydraulic conductance and stomatal conductance (b) are derived
1255 from published data and available in the supplementary database. The numbers above the boxplots in a and b denote the amount of unique source and site combinations at which the variables were averaged. Relative extractable water (c) and vapor pressure deficit (d) are derived from monthly ECMWF ERA5 reanalysis data extracted to 229 neotropical forest sites in South and Central America (1979-2019). Capital letters indicate a significant (p < 0.05, Tukey HSD) pairwise difference between the wet season, dry season and episodic drought values. When a group is not significantly different from the two other groups that are significantly different in the
1260 comparison, the capital letters are coupled.
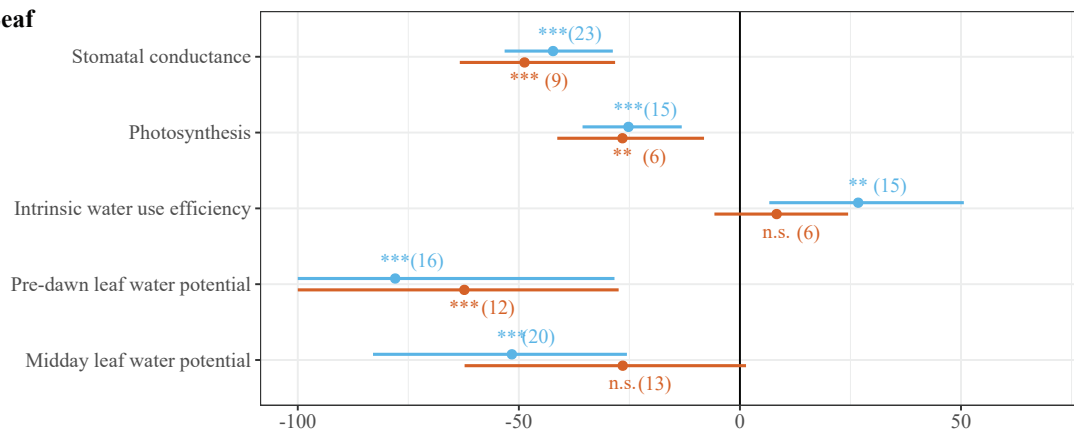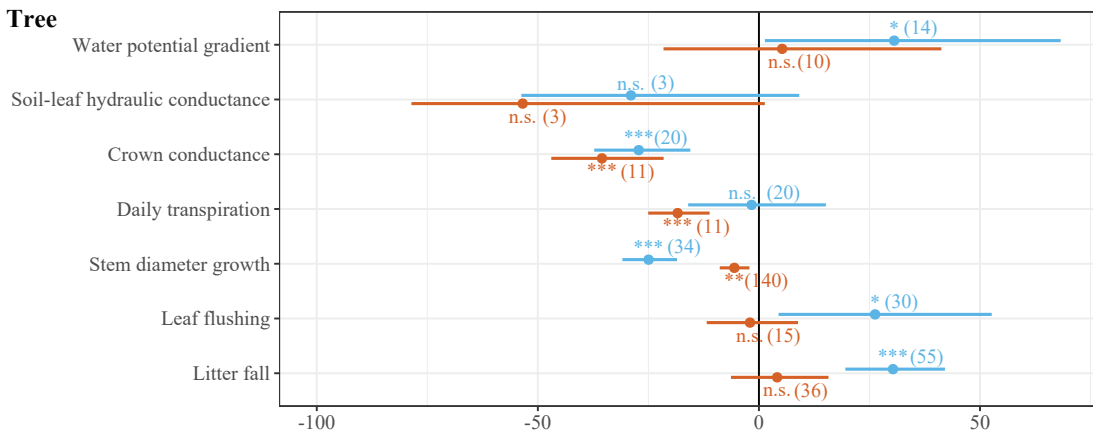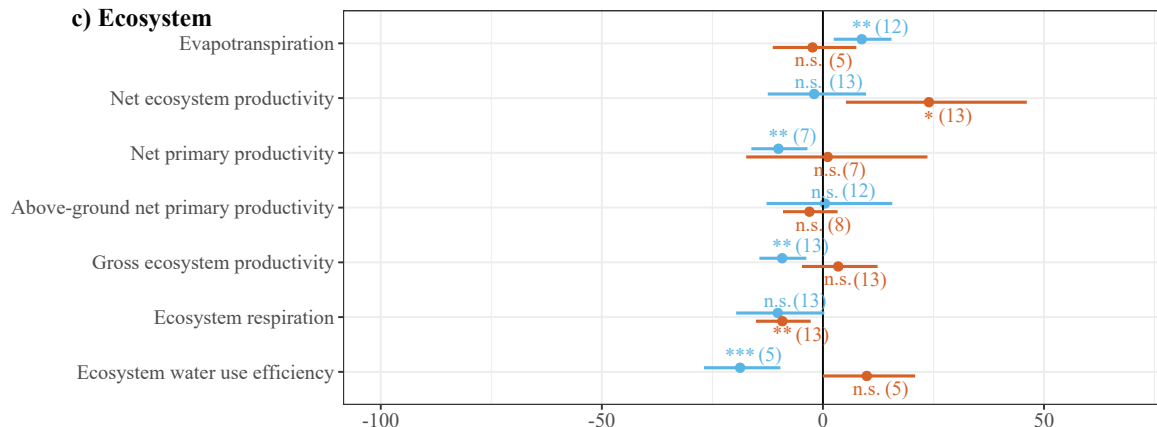
Figure 3: Meta-analysis results of leaf, tree and ecosystem scale responses to seasonal (blue) and episodic drought (red). The dots are the averages and the horizontal lines represent 95% confidence intervals of percentage change in leaf, tree and ecosystem scale performance. The confidence intervals for pre-dawn leaf water potential were cut off at -100% to prevent the x axis from inflating. Repeated measurements were used, therefore the variance of the response ratio is adjusted for by the correlation coefficient between the repeated measurements (Lajeunesse, 2011). The number of consulted studies or sites is provided in brackets. The significance symbols depict the p-value derived from a Random-effects model (* p < 0.001, ** p < 0.01, * p < 0.05) testing whether the effect size differs significantly from 0.**
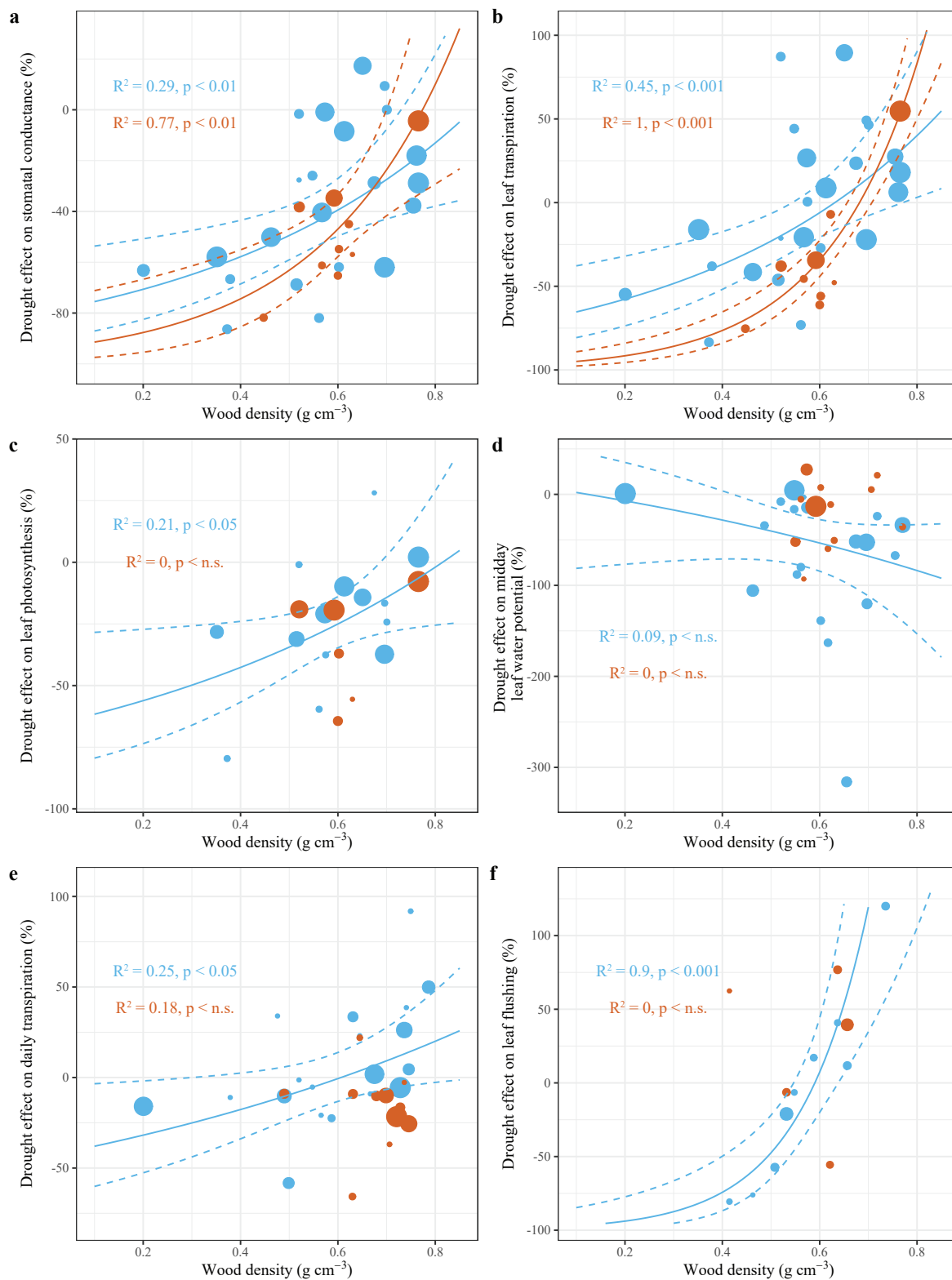
Figure 4: Effect size of leaf and tree scale responses to seasonal drought (black) and episodic drought (red) for different studies against the study averaged wood density. On the leaf-scale, studies with a low average wood density show a decline in stomatal conductance (a), potential leaf transpiration (b) and photosynthesis (c) in response to seasonal and episodic drought, while midday leaf water potential is not changed. On the tree scale, studies with a low average wood density show a decline in tree daily transpiration (e) and leaf flushing (f) to seasonal drought, but not episodic drought. The size of the points is determined based on the inverse of the sampling variance of the particular study (i.e. precision), showing larger points for more precise studies. The sampling variances are used to provide weights to the different studies in the Mixed-effect model. The test statistics are retrieved from a Mixed-effect model testing the significance of wood density as a moderator variable in the drought response. The solid line is the model prediction and the dashed lines are the 95% confidence intervals. Regression lines were only drawn if the relationship was significant ($p < 0.05$).