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# Transpiration on the rebound in lowland Sumatra

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## ABSTRACT

Following large-scale conversion of rainforest, rubber and oil palm plantations dominate lowland Sumatra (Indonesia) and other parts of South East Asia today, with potentially far-reaching ecohydrological consequences. We assessed how such land-use change affects plant transpiration by sap flux measurements at 42 sites in selectively logged rainforests, agroforests and rubber and oil palm monoculture plantations in the lowlands of Sumatra. Site-to-site variability in stand-scale transpiration and tree-level water use were explained by stand structure, productivity, soil properties and plantation age. Along a land-use change trajectory forest-rubber-oil palm, time-averaged transpiration decreases by 43 ± 11% from forest to rubber monoculture plantations, but rebounds with conversion to smallholder oil palm plantations. We uncovered that particularly commercial, intensive oil palm cultivation leads to high transpiration (827 ± 77 mm $yr^{-1}$), substantially surpassing rates at our forest sites (589 ± 52 mm $yr^{-1}$). Compared to smallholder oil palm, land-use intensification leads to 1.7-times higher transpiration in commercial plantations. Combined with severe soil degradation, the high transpiration may cause periodical water scarcity for humans in oil palm-dominated landscapes. As oil palm is projected to further expand, severe shifts in water cycling after land-cover change and water scarcity due to land-use intensification may become more widespread.

## 1. Introduction

Climate is governed by changes in atmospheric water vapour content and associated feedback mechanisms (Inamdar and Ramanathan, 1998; Held and Soden, 2000; Ellison et al., 2012). Terrestrial water fluxes from land surface to the atmosphere are dominated by plant transpiration (Jasechko et al., 2013; Good et al., 2015), which in turn is strongly affected by human land use. Land-cover change by forest conversion to agricultural systems usually substantially decreases (evapo)transpiration (Sampaio et al., 2007; Ellison et al., 2012; Silvério

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et al., 2015), which is associated with increases in land surface temperature (Alkama and Cescatti, 2016; Ellison et al., 2017; Sabajo et al., 2017) and decreases in regional precipitation (Bagley et al., 2014; Spracklen and Garcia-Carreras, 2015; Zemp et al., 2017a, 2017b). Potential effects of land-use intensification have received less attention so far. Recent research proposes that increases in cropland extent, productivity and intensification could influence climate through increasing (evapo)transpiration (Betts et al., 2013; Mueller et al., 2016, 2017).

Today, large-scale forest conversion mainly occurs in tropical regions, with currently highest rates in Southeast Asia and particularly in Indonesia (Hansen et al., 2013; Margono et al., 2014). In many Indonesian post-conversion landscapes, rubber and oil palm monocultures are dominant land-use types, while remaining rainforests have largely been selectively logged or degraded otherwise (FAO, 2014; Abood et al., 2015; Clough et al., 2016). Rubber has been cultivated in Indonesia since the early 1910s, formerly often in so-called 'jungle rubber' agroforests, a mixture of planted and spontaneously established trees of various ages (Gouyon et al., 1993; Joshi et al., 2003). Today, monocultural rubber plantations are much more widespread, and over the past 25 years oil palm monocultures have strongly increased in area (FAO, 2014; Abood et al., 2015; Clough et al., 2016).

Forest conversion to rubber and oil palm monocultures decreases biodiversity (Clough et al., 2016), ecological functioning (Barnes et al., 2014), soil fertility (Guillaume et al., 2015, 2016) and carbon storage (Guillaume et al., 2018) and leads to changes in microclimate (Meijide et al., 2018). In Amazonia, large-scale forest conversion to pasture and soy bean regionally decreased evapotranspiration, subsequently reducing downwind precipitation and resulting in more frequent and severe droughts (Bagley et al., 2014; Spracklen and Garcia-Carreras, 2015; Zemp et al., 2017a, 2017b). In contrast, woody perennial rubber and oil palm plantations in Southeast Asia could be more similar to forests regarding transpiration than Amazonian pastures or soy bean, and ecohydrological consequences thus potentially less severe. Previous studies found indications of quite high evapotranspiration from oil palm plantations (e.g. Radersma and de Ridder, 1996). Recent studies report very high annual transpiration and evapotranspiration from mature commercial, intensively managed oil palm plantations (Meijide et al., 2017; Manoli et al., 2018). It was indicated that smallholder oil palm plantations had lower transpiration than commercial plantations, but the study was restricted to short periods and did not provide annual estimates (Röll et al., 2015). Smallholder rubber plantations in lowland Sumatra had lower transpiration compared to adjacent smallholder oil palm plantations and also compared to commercial rubber plantations on the Asian mainland (Niu et al., 2017). To our knowledge, there are no previous studies in Southeast Asia that directly compare transpiration of different land-use types including rubber and oil palm with adjacent reference forest sites to allow a more comprehensive ecohydrological assessment. As oil palm is one of the most rapidly expanding crops worldwide (FAO, 2014), there is an urgent need to better understand the ecological consequences of its large-scale cultivation.

Establishing representative means of (evapo)transpiration for certain land-use types is one important aspect of ecohydrological studies; it can be accomplished by a high number of spatial replicates. Of further importance for analysing effects of land-cover and land-use change at the landscape level is to assess and understand variability, both within and across land-use types. Hourly, daily and seasonal fluctuations in transpiration at a certain site can commonly be well explained by micrometeorological variables (for rubber: Hardanto et al., 2017a; Niu et al., 2017; for oil palm: Röll et al., 2015; Meijide et al., 2017), sometimes in combination with soil moisture fluctuations (e.g., Tromp-van Meerveld and McDonnell, 2006; Hardanto et al., 2017a). Over larger time-scales, changes in transpiration can also be driven by functional changes in communities. Spatial, site-to-site variability in transpiration is often much harder to explain. Studies encompassing multiple sites are rare, and often there is a lack of data on potential explanatory variables describing e.g. differences in stand structure, productivity and soil. Available previous studies have related differences in transpiration among stands to diameter-dependent variables (e.g., basal area) as well as to specific leaf area (e.g., Cermák, 1989; Hatton et al., 1995; Roberts et al., 2001). In monoculture landscapes, plantation age was further found to substantially influence transpiration (Röll et al., 2015; Niu et al., 2017).

From 1990–2011, the lowlands of Sumatra underwent substantial land-use changes, losing about 45% of their forest area. In the same period, rubber plantations increased by almost 30%, and both smallholder and commercial oil palm plantations more than doubled in area (Clough et al., 2016; BPS, 2013; Margono et al., 2012; Villamor et al., 2014). Land-use change in lowland Sumatra is largely driven by profitability, and today oil palm is often the preferred land-use option (Clough et al., 2016; Kubitza et al., 2018). One main trajectory for the use of a certain unit of land leads from forest degradation over forest conversion to jungle rubber agroforest to monoculture rubber plantations to smallholder or commercial oil palm plantations (Clough et al., 2016; Drescher et al., 2016). It thus encompasses both land-cover change and land-use intensification as potential drivers of shifts in transpiration. Regarding the integrity of the hydrological cycle, this raises the question of how transpiration as a key ecohydrological process is affected along this linear main land-use change trajectory. At larger scales, current land-use dynamics in lowland Sumatra are mosaic-like and highly complex, further raising the question of how regional transpiration could be affected.

At 42 sites across the dominant land-use types of lowland Sumatra, Indonesia, we estimated transpiration using calibrated sap flux sampling schemes adapted to each land-use type. The land use types included selectively logged rainforests, jungle rubber agroforests, monoculture smallholder rubber plantations and smallholder and commercial oil palm plantations (Fig. 1). We (1) assessed annual stand-level transpiration and (2) analysed potential covariates to explore relationships with and discuss explanations for site-to-site variability in transpiration across land-use types. We (3) present a data-based concept on how land-use change along a trajectory forest-rubber-oil palm affects transpiration, and discuss what ecohydrological consequences this might have.

## 2. Materials and methods

### 2.1. Study region

The study region was Jambi Province (Sumatra, Indonesia, Fig. 1). From 1991–2011, annual temperature in Jambi was 26.7 ± 0.2 °C (mean ± SD, data from Sultan Thaha airport, Jambi). Annual precipitation in Jambi was 2235 ± 385 mm. A relatively dry season (below 120 mm monthly precipitation) usually occurs between June and September (Drescher et al., 2016). Temperature and precipitation were similar in the vicinity of our study sites (at approx. 100 km distance, **Figure** S-1).

Soil types at the study sites were well-drained loamy Acrisols dominated by kaolinites. Soils in the Harapan landscape (Fig. 1) are chromic Acrisols (loamic) and in the Bukit Duabelas landscape chromic Acrisols (clayic). In the Bukit landscape, soils contained more clay (31–60%) and were more saturated with base cations (20–38%) than in the Harapan landscape (26–37% clay and 10–28% base saturation) (Allen et al., 2015; Guillaume et al., 2015). Our study sites contain no pedosequences, as the soil parent materials and relief were very similar among sites and landscapes.

Our study encompassed 42 sites distributed over dominant land-use types of lowland Sumatra (Fig. 1): selectively logged rainforest (n = 8 sites), which is equivalent to 'primary degraded forest' (Margono et al., 2014), 'jungle rubber' (Gouyon et al., 1993) agroforests (n = 8), smallholder rubber plantations (n = 10), smallholder oil palm plantations (n = 14) and commercial oil palm plantations (n = 2). They were located at similar altitude and landscape positions (non-valley,

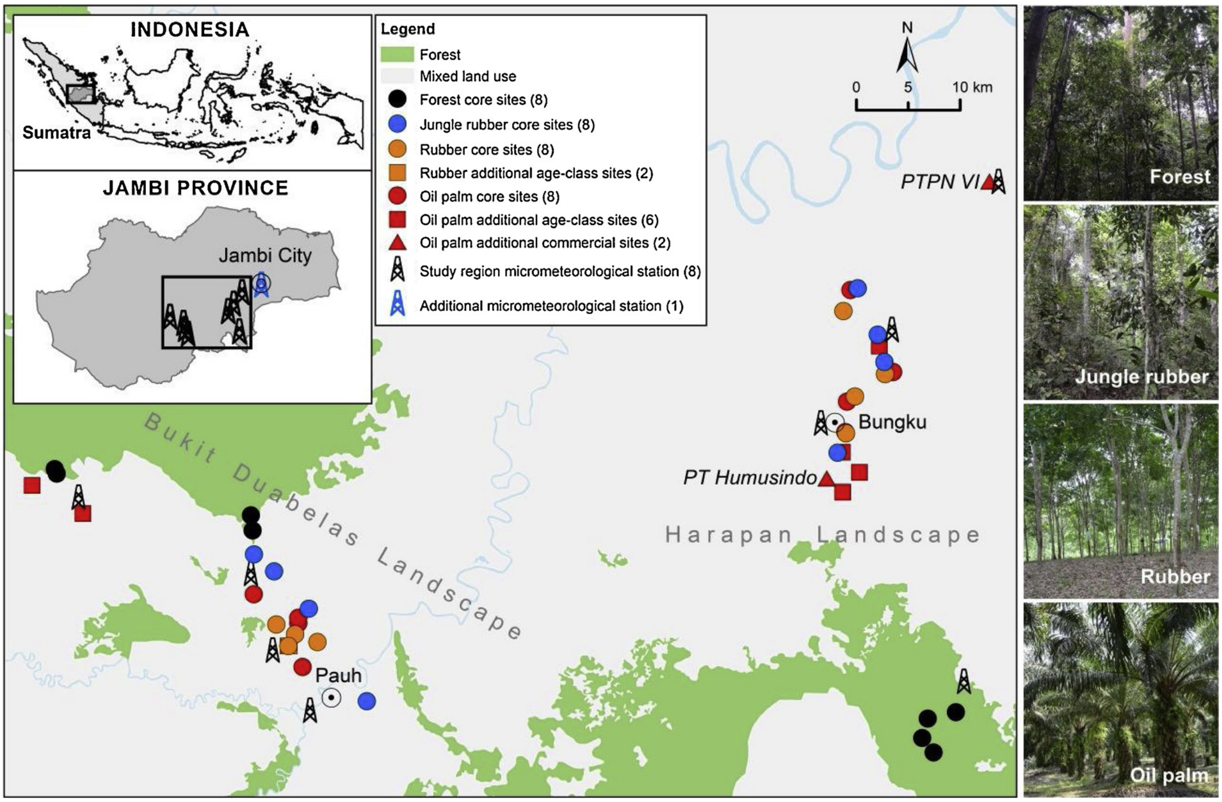

**Fig. 1.** Study sites in the lowlands of Jambi Province, Sumatra, Indonesia. 32 core sites in forests, jungle rubber agroforests and medium-aged smallholder monoculture rubber and oil palm plantations. Eight additional age-class sites in smallholder rubber and oil palm plantations and two additional sites in commerial oil palm plantations. Eight micrometeorological stations in the study region and one long-term station in the greater region (Province map).

moderate slopes, ˜70 m asl). The 42 sites comprised 32 'core sites', for which a large data set of stand structural, productivity, microclimate and soil related variables (**Table** S-1) were available within the framework of the EFForTS project (www.uni-goettingen.de/efforts; Drescher et al., 2016), as well as ten additional sites for which basic site and stand data (location, elevation, stand density, diameters, heights, age) had been recorded (**Table** S-2).

The eight core sites each in rubber and oil palm monocultures were 'productive' (i.e. fruit- or latex-yielding), medium-aged (8–16 years old) smallholder plantations (Drescher et al., 2016). Management among oil palm smallholder plantations was variable, but characterized by little fertilizer input (24–96 kg N $ha^{-1}$ $yr^{-1}$, Fan et al., 2015) compared to intensively managed, commercial oil palm plantations in the study region (240–456 kg N $ha^{-1}$ $yr^{-1}$, Fan et al., 2015; Teuscher et al., 2016). The ten additional sites encompassed two smallholder rubber and eight smallholder oil palm plantations along a gradient of plantation age as well as two commercial, intensively managed oil palm plantations (PTPN VI, PT Humusindo) (Fig. 1).

### 2.2. Sap flux derived daily transpiration

Sap flux measurements at 41 of 42 sites were performed between March 2013 and April 2014 (**Table** S-2, **Table** S-3). Measurements at the remaining site (PT Humusindo) were performed in October 2016, under similar environmental conditions and with identical methodology. At all 42 sites, we measured sap flux density ($J_S$, g $cm^{-2}$ $h^{-1}$) with thermal dissipation probes (TDP, Granier, 1985) in oil palm leaf petioles and in the outer xylem of tree trunks to derive daily stand transpiration ($E_t$, mm $d^{-1}$).

For oil palm, we used a species-specific set of parameters for the Granier sap flux equation (Granier, 1985) to estimate $J_S$; it had been derived in previous laboratory calibration experiments on petioles with simultaneous gravimetric measurements as a reference (Niu et al., 2015). We followed an oil-palm specific measurement scheme with simultaneous measurements in the petioles of 16 leaves on four different palms (Niu et al., 2015). At a mature oil palm site (PTPN VI), this approach yielded reasonable, i.e. 31–33% lower estimates for sap flux derived stand transpiration than for evapotranspiration derived from simultaneous eddy covariance measurements. The divergences are likely accounted for by canopy and soil evaporation, but could also partly root in estimation uncertainties associated with the sap flux measurements on a limited number of oil palms (Niu et al., 2015; Meijide et al., 2017) as well as in uncertainties associated with the eddy covariance technique at the PTPN VI site (e.g., regarding energy balance closure, Meijide et al., 2017) and in general (e.g., Teuling, 2018).

For rubber, we also applied a species-specific measurement scheme. It uses the original Granier equation parameters (Granier, 1985) for estimating $J_S$ (confirmed by calibration experiments), with simultaneous sap flux measurements on six trees (with two sensors each) per site (Niu et al., 2017).

For the structurally more heterogeneous forest and jungle rubber stands, we confirmed the applicability of the original Granier equation parameters in exploratory laboratory experiments in analogy to previous work (Niu et al., 2017). On average, we found close agreement between TDP-derived and reference gravimetric measurements when using the original Granier equation parameters ($J_S = 0.94 * J_G$; $R^2 = 0.92$; $P < 0.001$, where $J_G$ is the gravimetrically-derived sap flux density in g $cm^{-2}$ $h^{-1}$). This is in line with results from previous calibration studies on diffuse-porous dicot trees (Lu et al., 2004). We adjusted the above-described measurement scheme for rubber trees to the more heterogeneous stand structure of forest and jungle rubber by measuring on eight instead of six trees per site (also with two sensors per tree).

Four out of 32 core sites were 'long-term' $J_S$ monitoring sites (up to

1 year), one in each land-use type (**Table** S-4). At the remaining 28 core sites and at the ten additional sites, $J_S$ was successively measured for reduced periods (on average 27 days, **Table** S-5**)**. As sample trees, we chose predominant, dominant and co-dominant trees ('Kraft classes' 1–3, Kraft, 1984, see English description in Grala-Michalak and Kaźmierczak, 2011). In all land-use types, the minimum diameter at breast height (*DBH*, cm) for sample trees was 10 cm. At jungle rubber sites, sensors were evenly distributed among rubber and non-rubber trees. In accordance with a well-accepted observation that tree water use scales universally with tree size across species (Meinzer et al., 2005), we did not take into account tree species in our sap flux design in the very species rich land-use types forest and jungle rubber. Instead, we evenly chose individuals of relatively larger, medium and smaller *DBH* to assure well-balanced samples with respect to tree dimension. Nonetheless, the 259 sap flux sample trees across the 42 study sites commonly belonged to the most dominant species within each stand (assessed by species rank of relative contribution to total stand basal area), even in the very species-rich land-use types forest and jungle rubber (**Table** S-6). In jungle rubber (24–56 tree species per site), more than 80% of the sap flux sample trees belonged to the 10 most dominant species at the according sites. In forest (51–97 tree species per site), about 70% of the sample trees belonged to the 20 most dominant species (**Figure** S-2).

Sensor installation and protection were carried out in analogy to previous work on trees and palms in the study region (Niu et al., 2015, 2017). The sensors were connected to AM16/32 multiplexers connected to CR1000 data loggers (Campbell Scientific Inc., Logan, USA); signals were recorded every 30 s and averaged and stored every 10 min. To scale-up from TDP point measurements of $J_S$ to stand-scale $E_t$, stand water conductive areas (the summed-up tree cross sectional areas that are constituted by active xylem) were established for each site. For oil palm and rubber, methodological approaches were available (Niu et al., 2015; Niu et al., 2017). For forest and jungle rubber, in analogy to the approach for rubber (Niu et al., 2017), we measured radial patterns of $J_S$ with increasing depth into the xylem (0–8 cm, 1 cm resolution) with heat field deformation sensors (HFD, ICT International, Armidale, Australia; Nadezhdina et al., 2012) on ten sample trees per land-use type, in parallel to TDP measurements in the outer xylem. By averaging daily $J_S$ for each of the eight HFD measurement depths (from at least two weeks per tree), radial patterns of $J_S$ were established. They were then normalized by the value at the standard TDP measurement depth and used to calculate the adjusted water conductive area ($WCA_{\text{adj}}$, cm$^2$) for each sample tree, i.e. the diameter-dependent basal area corrected for radial differences in $J_S$ in relation to the standard TDP measurement depth (see Niu et al., 2017 for methodological details). This approach yielded significant relationships between *DBH* and $WCA_{\text{adj}}$ for both rubber and non-rubber trees at jungle rubber sites as well as for non-rubber trees at forest sites (**Methods** S-1). Using stand density and *DBH* distribution data of the study sites subsequently allowed calculating stand water conductive areas ($WCA_{\text{stand}}$).

To calculate daily $E_t$ estimates for each site, $J_S$ day-sums of all sensors running simultaneously were averaged and multiplied by the respective $WCA_{\text{stand}}$. Commonly, only days with more than 13 (oil palm), ten (rubber), and 14 (jungle rubber and forest) sensors running simultaneously were included due to high associated estimation errors at smaller sample sizes. Using these sampling schemes, $E_t$ estimates in the heterogeneous land-use types forest and jungle rubber are associated with sample size-induced estimation errors of approx. 30% (Granier et al., 1996), while potential errors for rubber and oil palm are reported to be substantially smaller (< 15%, Niu et al., 2015, 2017). Days with severe data abnormalities or data gaps larger than two hours were excluded from the respective datasets; to fill data gaps up to two hours, linear interpolation of hourly values was performed before deriving daily sums.

### 2.3. *Microclimate, soil moisture and reference potential evapotranspiration*

We monitored key micrometeorological variables at eight open-area reference meteorological stations in the vicinity of the study sites (Fig. 1), as well as below-canopy microclimate and soil moisture and temperature with 32 micrometeorological stations at the center of each core site.

At the 32 below-canopy stations, below-canopy air temperature and relative humidity were measured. Simultaneously, soil moisture was monitored at 0.3 m depth below the soil surface (Meijide et al., 2018). To derive a complete data series of soil moisture for the study region (**Figure** S-3), we averaged data from all stations running simultaneously.

The eight meteorological reference stations near our study sites were located at similar altitude (60 m ± 15 m a.s.l.) in open terrain. Air temperature and relative humidity were measured at 2 m height with a thermohygrometer (type 1.1025.55.000, Thies Clima, Göttingen, Germany). Wind speed was measured with an anemometer (Thies Clima) at 4 m height. A net radiation sensor (NR Lite2, 200 − 100,000 nm, Kipp & Zonen, Delft, The Netherlands) and shortwave radiation sensor (CMP3 Pyranometer, Kipp & Zonen) were installed at 3 m. Measurements were taken every 15 s and averaged and stored every 10 min on a DL16 logger (Thies Clima). Recorded micrometeorological variables were the basis for deriving daily values of potential evapotranspiration ($E_o$, mm d$^{-1}$) with the Priestley-Taylor equation (Priestley and Taylor, 1972) using the R package Evapotranspiration (Guo and Westra, 2016). To obtain a complete (Jan 2013 – Jan 2015) $E_o$ series as a reference for sap flux derived $E_t$ and as a basis for modelling annual values, we used an almost complete data series from one of our climate stations ('Reki station') and gap-filled missing values with the average of all other stations running simultaneously (distance 30–90 km, < 25% of daily data gap-filled). This seemed justified because daily $E_o$ from all stations were highly and significantly correlated to $E_o$ from Reki when running simultaneously (average divergences < 10%, **Figure** S-4). Annual $E_o$ was 1408 mm in 2013 and 1310 mm in 2014.

More basic, but longer-term measurements of temperature and precipitation were further available from a station at Jambi Airport (1991–2014, approx. 100 km east of our sites) (Fig. 1**)**. The station is operated by the Indonesian Weather Service BMKG.

### 2.4. *Annual transpiration*

Temporal variability of $E_t$ is generally largely explained by day-to-day fluctuations in micrometeorological driving variables, given that soil moisture remains non-limiting (i.e. not too low and not too high) (Oren et al., 1999; O'Brien et al., 2004; Kume et al., 2007; Hardanto et al., 2017a). Our study period (Jan 2013 – Jan 2015) at 41 of the 42 study sites ended before the 2015 ENSO event, while measurements at the remaining site (PT Humusindo) were performed well after the ENSO event, in October 2016. Environmental conditions during the respective study periods were representative of long-term average climatic conditions regarding temperature and precipitation (**Figure** S-1). Soil moisture remained relatively stable at sufficiently high levels over our study period and at all sites to be considered non-limiting for tree water use (**Figure** S-3**, Table** S-7). The sites were not flooded during the sap flux measurements.

We consequently followed a linear regression approach between daily $E_t$ (sap flux derived) and potential evapotranspiration $E_o$ derived from simultaneous micrometeorological measurements to estimate annual $E_t$. It is similar to previous cropping coefficient approaches for calculating crop evapotranspiration (Allen et al., 1998) and was previously applied for estimating annual $E_t$ of two of the oil palm (Meijide et al., 2017) and one of the rubber plantations (Niu et al., 2017) in our study. In those two oil palm plantations, the approach yielded estimates for the contribution of $E_t$ to total annual evapotranspiration (derived from simultaneous eddy covariance measurements) of 7% (very young plantation) and 68% (mature commercial plantation) (Meijide et al., 2017). These results were interpreted as ecologically reasonable considering additional evaporation from soil and canopy (including leaf axils of mature palms, Tarigan et al., 2018), and, in the case of the very young plantation, the unassessed transpiration of a dense grass layer surrounding the planted, still very small oil palms (Meijide et al., 2017). Exploratory analyses with data from the four long-term monitoring plots showed that annual $E_t$ derived from our simple linear regression approach differed less than 5% from several tested non-linear approaches (e.g. logarithmic, Weibull, Mitscherlich), with the advantage of higher robustness in case of study sites with relatively few available daily $E_t$ values for model fitting.

At each site, we used the mentioned $E_o$ time series for the study region (**Figure** S-3) and performed linear regressions (forced through origin) of daily TDP-derived $E_t$ vs. $E_o$ from the corresponding days. Resulting $E_t$ /$E_o$ ratios (i.e. the slopes of the regressions) were subsequently multiplied by annual $E_o$ to obtain estimates of annual $E_t$ (mm yr$^{-1}$). This approach of using linear $E_t$/$E_o$ ratios to extrapolate to annual $E_t$ rates accounts for potential differences in climatic driving variables (in our study represented by $E_o$) among the non-simultaneous sap flux measurement periods at the 42 sites. Exploratory Monte-Carlo analyses (with 10,000 iterations) using the data from the long-term monitoring plots (plot codes BF3, BJ5, BR3, BO3) and systematically varying the sampling size from 1 up to 365 consecutive days showed that our linear regression approach of deriving annual $E_t$ estimates for the remaining 28 study sites based on reduced measurement periods (13–66 days of usable data, **Table** S-5) is associated with potential divergences of 15–20% compared to using fully measured data.

Our linear regression approach yielded strong linear relationships ($R^2 > 0.92$, $P < 0.001$) between daily $E_t$ and $E_o$ for all 42 study sites, based on 45 ± 11 days (mean ± SE) of simultaneous measurements per site (**Table** S-5**)**. Comparing day-to-day measured $E_t$ with $E_o$-based modeled $E_t$ series shows good agreement across sites and land-use types (**Figures** S-5 and S-6**)**. Divergences between measured and modelled mean daily $E_t$ were consistently below 5% and RMSEs mostly below 20% (max. 28%). Parametric bootstrapping suggests low uncertainties (expressed by SEs) of annual $E_t$ estimates, less than 5.2% at all sites (**Table** S-5).

A study from the same region reported about 20% reductions in monoculture rubber $E_t$ due to gradual leaf coverage reductions of 30–60%, with the partial leaf shedding period lasting approx. three months (Niu et al., 2017). Because of this, we firstly corrected all annual monoculture rubber $E_t$ estimates that base on measurements under fully-leaved conditions (five core sites and two additional sites) by a shedding period of 86 days, with $E_t$ reductions of 20% (in analogy to observations at the rubber long-term monitoring site BR3, also see **Figure** S-3). Secondly, for two monoculture rubber sites among the 32 core sites (plot codes HR2 and HR3, **Table** S-3) the $E_t$/$E_o$ ratios were linearly corrected before extrapolation to annual $E_t$, because partial leaf shedding occurred during the entire respective sap flux measurement periods. Based on the study by Niu et al. (2017), we multiplied the two respective $E_t$/$E_o$ ratios by 1.25 (i.e. accounting for on average 20% lower $E_t$ during partial leaf shedding, **Table** S-5). Assuming about 20–40% shedding at our sites (visual assessment), this magnitude of correction is in line with research on several tropical tree species showing a similar (and linear) relationship between degree of shedding and $E_t$ (Kunert et al., 2010).

### *2.5. Covariates to explore site-to-site variability in transpiration*

We hypothesized that site-to-site variability in stand transpiration $E_t$ (or mean tree water use *WU*) is explained by stand structural, productivity and soil variables. For our 32 core sites, a large set of covariates were available to test this hypothesis. General site and stand characteristics had previously been published. They include mean stand diameter and height, above- and belowground biomass (Kotowska et al., 2015) and estimates of canopy gap fraction (Drescher et al., 2016) (**Table** S-3**)**. Further available covariates were estimates of above- and belowground net primary productivity (Kotowska et al., 2015) as well as a variety of classic pedological parameters (e.g., pH, bulk density, nitrogen- and carbon-related variables; Allen et al., 2015; Guillaume et al., 2015) and annual means of soil moisture and temperature (Clough et al., 2016). Furthermore, basic microclimatic variables (e.g., average annual below-canopy temperate) were available from each of the 32 sites (Clough et al., 2016; Meijide et al., 2018).

As additional, previously unpublished stand structural variables, estimates of canopy cover and different effective leaf area indices (*LAI*, m$^2$ m$^{-2}$) were calculated from hemispherical photographs (Drescher et al., 2016) with CAN-EYE (Version 6.4.6, INRA Centre de recherche PACA, Avignon, France). Simultaneously to taking hemispherical photographs, below-canopy photosynthetically active radiation (*PAR*, μmol s$^{-1}$ m$^{-2}$) and *PAR* at an open reference site were measured with LI-190SA quantum sensors connected to LI-Cor 250 A light meters and LI-1400 data loggers (Li-Cor Biosciences, Lincoln, NE, USA) to estimate canopy light transmission (%).

Based on nine systematically distributed single terrestrial laser scans made at 29 of the 32 core sites (notably: in 2016; three sites missing), a stand structural complexity index (*SSCI,* Ehbrecht et al., 2017) and the effective number of canopy layers (*ENL,* Ehbrecht et al., 2016) were calculated. The computations were based on 3D points clouds obtained using a FARO Focus 3D terrestrial laser scanner (Faro Technologies Inc., Lake Marry, USA).

Soil samples taken from different horizons were analysed regarding their carbon (C) and nitrogen (N) content, their C/N ratio and the abundance of stable isotopes ($\delta\,^{13}C$, $\delta\,^{15}N$) (Guillaume et al., 2015).

### *2.6. Shifts in local and regional transpiration*

One main land-use trajectory for a certain unit of land in lowland Sumatra leads from forest degradation over forest conversion to jungle rubber to monoculture rubber plantations to smallholder or commercial oil palm plantations (Clough et al., 2016; Drescher et al., 2016). To examine shifts in transpiration along this linear trajectory, we applied the annual $E_t$ estimates from the 42 study sites. For forest and jungle rubber agroforests (non-rotational systems), we assumed steady-state $E_t$ over time. For the rubber and oil palm monoculture plantations (rotation systems), we provide time-averaged $E_t$ values over rotation cycles of 20 (rubber) and 25 years (oil palm); they base on age-$E_t$ relationships as derived from the analysis of 14 smallholder oil palm and 10 smallholder rubber plantations along a gradient of plantation age (including the eight core sites each, see *Statistical analyses*). We further expanded our measurement-based $E_t$ estimates by literature values from previous studies in undisturbed tropical lowland forests (average of 12 sites in Kunert et al., 2017; Kume et al., 2011; Bruijnzeel, 1990; Lion et al., 2017).

We combined stand-level $E_t$ in dominant land-use types (as presented in the linear trajectory) with area fraction estimates for 1990 and 2011 (Clough et al., 2016) to estimate regional shifts in transpiration for lowland Sumatra. We further su**b**-categorized forests into ‘undisturbed’ and ‘selectively logged’ forests using data from Margono et al. (2012). The category oil palm was further subdivided into ‘smallholder’ and ‘commercial’ plantations, using data from the Statistical Office of Indonesia (BPS, 2013). We applied the value of jungle rubber agroforests for all ‘intermediate’ land-use types (e.g., fallows, regrowth). Due to a lack of any further information, for our calculations all thus far not classified ‘other areas’ were assigned the transpiration value of the average of all other land-use types.

### *2.7. Statistical analyses*

To ensure the stability of our linear regression approach between daily transpiration $E_t$ (sap flux derived) and potential evapotranspiration $E_o$ (Priestly-Taylor-derived) for estimating annual transpiration at our study sites, and to provide uncertainty estimates for annual $E_t$, we performed parametric bootstrapping (with the R package 'boot', Canty and Ripley, 2017) with 50,000 iterations and derived means and standard errors. In analogy to previous work (Meijide et al., 2017), we bootstrapped the linear relationship between $E_t$ and $E_o$ (forced through the origin) (**Table** S-5).

To test for differences in mean annual $E_t$ (and *WU*) among land-use types and in the forest-rubber-oil palm land-use change trajectory, we applied linear regressions with land-use type as the categorical variable. We tested for overall significance with ANOVA ($P < 0.05$) and for significant differences among groups with a post-hoc Tukey-LSD test. The data sets were log-transformed for the ANOVA to minimize patterns in residuals.

To identify and analyse potential covariates for explaining site-to-site variability in transpiration, we first applied univariate linear regression models and tested all available single variables. We further applied multiple linear regression models ($E_t = a + b_1*x_1 + b_2*x_2 + \ldots + b_n*x_n$, where a is the intercept, x are the different available variables and b are the parameters to be fitted) and tested different blocks of variables from the categories stand structure, productivity and soil (with and without statistical interaction) in a 'brute-force' approach using the R package leaps (Lumley and Miller, 2009). In our study, only significant ($P < 0.05$) models of substantial explanatory power ($R^2 > 0.60$) are presented. They are ordered from lower to higher Akaike information criterion (AIC) values and provided with F-statistics and degrees of freedom (DF). Models were further examined regarding patterns in residuals, leverage and robustness.

To examine the influence of plantation age on $E_t$, we separately pooled the data from all available smallholder rubber (n = 10 sites) and smallholder oil palm plantations (n = 14), respectively. We normalized $E_t$ values by the respective means of the eight core sites each and plotted them against plantation age. We then fitted exponential functions ($y = y_0 + A*exp(R_0*x)$, where $y_0$, $A$ and $R_0$ are the parameters to be estimated) to each of the two datasets.

Statistical analyses were performed with R 3.1.1 (R Core Team, 2014). For graphing, Origin 8.5 (Origin Lab, Northampton, MA, USA) was used.

## 3. Results

### 3.1. Transpiration among land-use types

Annual transpiration ($E_t$, mm yr$^{-1}$) for the 32 core sites decreased in the sequence selectively logged forest (589 ± 52 mm yr$^{-1}$, mean ± SE), medium-aged smallholder oil palm plantations (543 ± 24 mm yr$^{-1}$), jungle rubber agroforests (521 ± 80 mm yr$^{-1}$) and medium-aged smallholder monoculture rubber plantations (391 ± 38 mm yr$^{-1}$) (Fig. 2). Mean $E_t$ differed significantly among land-use types (ANOVA, $P < 0.05$). $E_t$ in rubber monoculture was lower than in forest and oil palm (post-hoc LSD test, $P < 0.05$), while jungle rubber $E_t$ was intermediate. Jungle rubber was characterized by at least 37% higher site-to-site variability in $E_t$ than the other land-use types and encompassed the sites with the highest (995 ± 43 mm yr$^{-1}$, mean ± SE from bootstrapping) and lowest $E_t$ (264 ± 14 mm yr$^{-1}$) (Fig. 2**, Table** S-3).

### 3.2. Site-to-site variability in transpiration

Only small parts of the observed variability in $E_t$ among the 32 core sites (Fig. 2) were explained using univariate regressions and the large set of potential covariates (**Table** S-8). A multiple linear regression model allowing for interactions among stand structural, productivity and soil variables explained 73% of variability in $E_t$. Stand density, mean tree diameter and topsoil stable $\delta\ ^{15}N$ isotopic signature were significant covariates ($P < 0.001$, Table 1).

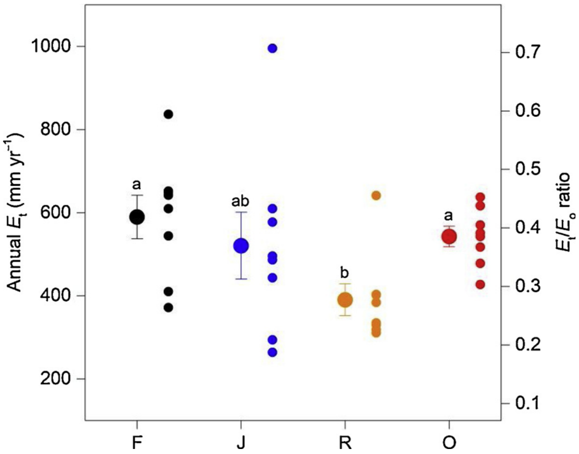

**Fig. 2.** Stand-level transpiration across land-use types. Annual transpiration ($E_t$, mm yr$^{-1}$) and the ratio of $E_t$ to potential evapotranspiration ($E_t$ / $E_o$) of eight core sites each in forest (F), jungle rubber agroforests (J) and medium-aged smallholder rubber (R) and oil palm plantations (O). Overall means (and standard errors) are presented as large dots (with bars). Significant differences between the groups as based on an ANOVA with post-hoc LSD test are indicated by different letters.

We further analysed potential covariates of mean tree water use *WU* across the 32 sites (**Table** S-9). Crown projection area per tree explained 91% of the variability in *WU* ($P < 0.001$). Several further stand structural variables (e.g. mean tree diameter, stand density, fine root biomass and gap fraction) also explained much of the observed variability in *WU* ($R^2 > 0.6$, $P < 0.001$). *WU* was further positively related to productivity-related variables, particularly per-tree total and aboveground net primary productivity (*NPP)* ($R^2 > 0.85$, $P < 0.001$) (Table 1).

### 3.3. Influences of plantation age and management

For both rubber and oil palm smallholder plantations (combined data from core sites and additional sites, Fig. 1), we observed strong increases in annual $E_t$ up to an age of about seven years. $E_t$ subsequently maintained a steady state regardless of plantation age (Fig. 3). Of site-to-site variability in $E_t$, 51% (rubber, n = 10) and 80% (oil palm, n = 14) were explained by plantation age ($P < 0.001$). In intensively managed, commercial oil palm plantations (PTPN VI and PT Humusindo), $E_t$ was on average 73% higher than in smallholder plantations of similar age (Fig. 3).

### 3.4. Shifts in transpiration at the local and regional scale

The previously introduced linear main land-use trajectory for a certain unit of land in lowland Sumatra (forest-rubber-oil palm) goes along first with a decrease and then a rebound of $E_t$ (Fig. 4). Conversion of selectively logged forests to monoculture rubber plantations (land-cover change) decreases $E_t$ by 43 ± 11%. Eventual land-cover change to oil palm leads to a rebound in transpiration: conversion to smallholder oil palm almost raises $E_t$ back to the level of forests, while land-use intensification to commercial oil palm increases $E_t$ by a factor of 1.7 compared to smallholder oil palm, thus even exceeding $E_t$ in logged forests (Fig. 4).

At the regional scale, land-use dynamics are more complex than depicted in the 'local' linear main trajectory. Combining stand-level $E_t$ of dominant land-use types with area fraction estimates for lowland Sumatra suggests 9% decreases in regional $E_t$ from 1990 to 2011 (Table 2). The predicted continuing conversion to oil palm and particularly land-use intensification to commercial oil palm will likely

**Table 1**
Covariates to explore site-to-site variability in stand-level transpiration ($E_t$) and tree-level water use (*WU*). Results from linear regression analyses among the 32 core sites based on variables related to stand structure, productivity and soil characteristics.

| | | Covariates | | | | Statistics | | |
|---|---|---|---|---|---|---|---|---|
| | Stand structure | Productivity | Soil | AIC | $R^2$ | P | F-stat | DF |
| Stand transpiration $E_t$ | stand density * diameter$_{mean}$[3] | – | * $^{15}$N signature[3] | −55.5 | 0.70 | 0.0002 | 7.1 | 7, 21 |
| Mean tree water use *WU* | per-tree crown area | – | – | 251.3 | 0.91 | 2.20E-16 | 321.4 | 1, 30 |
| | diameter$_{mean}$[1] | – | – | 256.7 | 0.90 | 2.20E-16 | 266.7 | 1, 30 |
| | – | per-tree NPP$_{total}$[1] | – | 261.1 | 0.88 | 1.43E-15 | 228.5 | 1, 30 |
| | – | per-tree NPP$_{aboveground}$[1] | – | 263.2 | 0.87 | 3.81E-15 | 212.2 | 1, 30 |
| | per-tree necromass$_{fineroot}$[1] | – | – | 283.1 | 0.76 | 4.46E-11 | 100.2 | 1, 30 |
| | mean tree height[2] | – | – | 292.0 | 0.69 | 3.00E-09 | 68.7 | 1, 30 |
| | canopy cover[2] | – | – | 292.1 | 0.68 | 3.13E-09 | 68.4 | 1, 30 |
| | stand density[2] | – | – | 293.2 | 0.67 | 5.34E-09 | 65.0 | 1, 30 |
| | per-tree biomass$_{fineroot}$[1] | – | – | 296.9 | 0.63 | 3.19E-08 | 54.5 | 1, 30 |

– = not significant.
* = multivariate regression with interaction.
[1] positive influence.
[2] negative influence.
[3] interaction.

rebound regional $E_t$. In comparison to times when the forests of Sumatra were still more extensive and undisturbed as a baseline (e.g. 1932), regional reductions in $E_t$ until 2011 are estimated to be much larger (**Table** S-10).

## 4. Discussion

### 4.1. *Transpiration among land-use types*

Annual transpiration at our 32 core sites decreased in the sequence selectively logged forest, medium-aged smallholder oil palm plantations, jungle rubber agroforests and medium-aged smallholder monoculture rubber plantations (Fig. 2).

Mean $E_t$ of our forest sites (589 ± 52 mm $yr^{-1}$) was considerably lower than in undisturbed, old growth tropical lowland rainforests in Amazonia and South East Asia (1023 mm $yr^{-1}$, mean of 12 sites, Bruijnzeel, 1990; Kume et al., 2011; Kunert et al., 2017; Lion et al., 2017). Among these, Pasoh Forest Reserve in Malaysia is located closest to our study region; there, $E_t$ was estimated at 801 mm $yr^{-1}$ (Lion et al., 2017). In Amazonian undisturbed forest, it was found that large emergent canopy trees account for up to 71% of $E_t$ (Kunert et al., 2017). Such trees were largely absent in the selectively logged forests (Clough et al., 2016; Drescher et al., 2016) where our study sites were located. It thus seems reasonable that we found lower $E_t$ than the mean of previous studies in undisturbed tropical forests.

Jungle rubber was characterized by high site-to-site variability in $E_t$ and encompassed both the sites with the highest and lowest $E_t$. Mean jungle rubber $E_t$ (521 ± 80 mm $yr^{-1}$, or on average 1.4 mm $day^{-1}$) appears centred within a variety of tropical agroforestry and reforestation system estimates from previous studies (0.5–2.5 mm $day^{-1}$, Cienciala et al., 2000; Dierick and Hölscher, 2009; Dierick et al., 2010; Köhler et al., 2014; Hardanto et al., 2017b).

Medium-aged smallholder rubber monoculture plantations had the lowest mean $E_t$ (391 ± 38 mm $yr^{-1}$), significantly lower than forests and smallholder oil palm (Fig. 2). The lower transpiration in rubber plantations is in line with 33–53% lower *NPP* (Kotowska et al., 2015), and with 20–80% lower basal area, biomass and leaf area compared to forests (**Table** S-3). Periodically occurring partial leaf shedding during dry periods with reductions of $E_t$ of 30–70% contributes to low annual rubber $E_t$ (Niu et al., 2017). At first sight, our low rubber $E_t$ estimate contrasts reports of high rubber evapotranspiration from mainland Asia (Tan et al., 2011). However, available estimates of annual $E_t$ from mainland Asia are only 10–20% higher than our mean rubber estimate (Kobayashi et al., 2014; Giambelluca et al., 2016). Potential reasons for divergences are 11–14% higher stand densities and higher management intensity at the mainland sites as well as higher evaporative demand in mainland Asia compared to equatorial Indonesia (Niu et al., 2017).

Mean $E_t$ in medium-aged smallholder oil palm plantations (543 ± 24 mm $yr^{-1}$) was only 8% lower than in forest (Fig. 2), despite 85% lower total biomass (Kotowska et al., 2015). Annual evapotranspiration of oil palm plantations derived from eddy covariance measurements was also found to be high, with rates similar to tropical forests (Meijide et al., 2017; Manoli et al., 2018). Mean per-tree water use *WU* of oil palms was substantial (108 ± 6 kg $d^{-1}$, mean ± SE

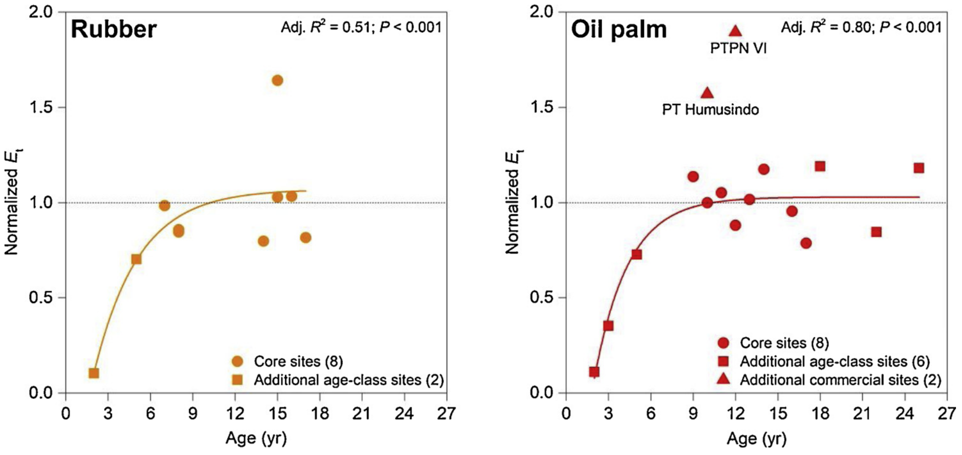

**Fig. 3.** Transpiration as influenceced by plantation age in rubber and oil palm plantations. Annual transpiration ($E_t$) normalized by previously presented means of eight core sites each in rubber and oil palm plantations (Fig. 2), plotted against plantation age. Exponential functions were fitted to each dataset (excluding the commercial oil palm plantations PTPN VI and PT Humusindo).

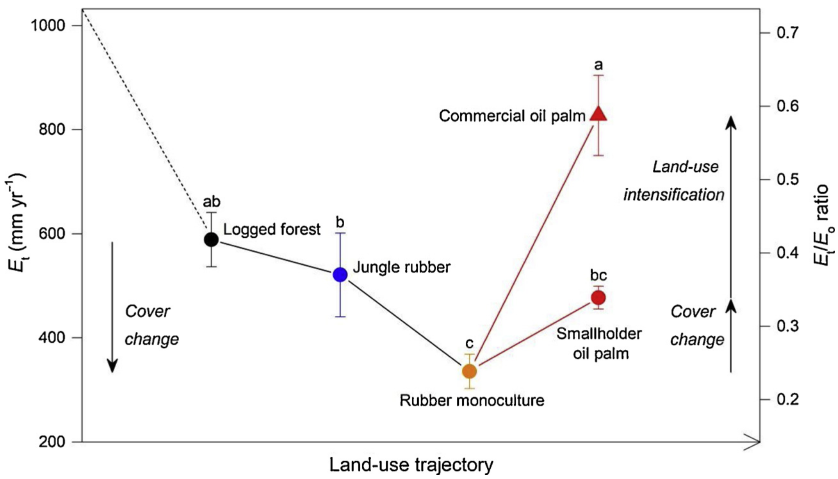

**Fig. 4.** Data-based concept of annual transpiration ($E_t$) changes along a forest-rubber-oil palm trajectory. Equivalent changes in the ratio of $E_t$ to potential evapotranspiration ($E_t$ / $E_o$). Values for rubber and oil palm monoculture systems are age-adjusted averages over rotation cycles, while 'steady state' transpiration over time is assumed for forests and agroforests. We used mean $E_t$ of 12 undisturbed tropical lowland rainforests across the tropics (Table 2) as the starting point of the trajectory. Bars indicate bootstrapping-derived standard errors. Significant differences in $E_t$ among land-use types (ANOVA with post-hoc LSD-test) are indicated by different letters.

among sites) in our study, four- to five-times higher than in the other land-use types (**Table** S-3). High $E_t$ and *WU* in oil palm plantations go along with very high *NPP* (47% higher than at forest sites, Guillaume et al., 2018). Oil palm *NPP* is to 58% allocated to fruit yield (Guillaume et al., 2018), making it the globally highest-yielding oil crop.

### 4.2. Site-to-site variability in transpiration

Site-to-site transpiration varied considerably across the 32 core sites (Fig. 2). Using univariate regressions, only small parts of the observed variability in $E_t$ were explained (**Table** S-8). Basic stand structural variables, more complex indices derived from terrestrial laser scans (*SSCI*, *ENL*) as well as soil moisture alone did not explain site-to-site variability in $E_t$. While it is undisputed that spatial variations in soil moisture in general have significant control over $E_t$ (Berry et al., 2005; Tromp-van Meerveld and McDonnell, 2006; Hardanto et al., 2017a), soil moisture did not significantly influence $E_t$ in our study because of high precipitation (Merten et al., 2016) and loam and clay Acrisol soil properties (Allen et al., 2015) at the study sites. Soil moisture fluctuated little among days and seasons and remained relatively high on average and at all measurement stations in the study region throughout the study period (**Table** S-7) due to the absence of prolonged periods without precipitation (**Figure** S-3). Exploratory analyses showed no significant influence of soil moisture fluctuations on $E_t$ within or across land-use types at any time scale (e.g. hourly, daily, monthly), which is in line with previous results from rubber and oil palm long-term monitoring sites in the study region (Niu et al., 2015, 2017).

A multiple linear regression model allowing for interactions among strand structural, productivity and soil variables explained 73% of variability in $E_t$, with the variables stand density, mean tree diameter and topsoil stable $\delta\ ^{15}N$ isotopic signature as significant covariates (Table 1). Stand density and mean tree diameter (or basal area) are usual suspects for explaining variability in $E_t$ (e.g. Cermák, 1989; Hatton et al., 1995; Cienciala et al., 2000); as such, with site-specific upper limits, $E_t$ tends to be higher in stands with a higher density and a larger mean diameter. Soil $\delta\ ^{15}N$ has, to our knowledge, not been connected to $E_t$ in previous studies. Its ecological interpretation is thus more difficult; in our case, it likely functions as an indicator of disturbance. As such, higher soil $\delta\ ^{15}N$ have been related to lower canopy cover (Evans and Ehleringer, 1993) and a higher degree of soil disturbance (Matson et al., 1987) and erosion (Martinelli et al., 1999, by bringing up deeper soil layers with a higher $\delta^{15}$N signature). It can potentially also be related to fertilization. However, further in-depth studies will be needed to comprehensively address the role of soil $\delta\ ^{15}$N as an indicator for ecohydrological processes.

We further expected a productivity-related variable to be part of significant (multiple) linear $E_t$ models. However, due to the exceptionally high water use efficiency of oil palm (*NPP* divided by $E_t$), these models do not hold across land-use types. For smallholder oil palm plantations, mean water use efficiency was 44% higher (3.1 g C

**Table 2**

Land-use types, area fractions and shifts in regional transpiration between 1990 and 2011. Ratios of transpiration to potential evapotranspiration ($E_t$ / $E_o$) and transpiration ($E_t$, mm yr$^{-1}$) as presented in our study for selectively logged forests, jungle rubber agroforests and monoculture rubber and oil palm plantations in lowland Sumatra. Time-averaged $E_t$ over the respective common rotation cycles are presented for rubber and oil palm monoculture systems.

| Annual precipitation (P) 2199 mm<br>Annual potential evapotranspiration ($E_o$): 1408 mm<br>P/$E_o$ ratio: 1.56 | $E_t$ / $E_o$<br>Ratio<br>Time-averaged means | $E_t$ (mm yr$^{-1}$)<br>Measurements in our study<br>(mean ± SE) | 1990<br>area fraction (%)<br>Adjusted from Clough et al., 2016 | 2011<br>area fraction (%)<br>Adjusted from Clough et al., 2016 |
|---|---|---|---|---|
| Undisturbed forest | 0.73 *1 | 1023 *1 | 17.9 *3 | 9.5 *3 |
| Logged forest | 0.42 | 589 ± 52 | 48.6 *3 | 27.1 *3 |
| Intermediate land-use, jungle rubber | 0.37 | 521 ± 80 | 3.4 | 16.4 |
| Small-holder rubber | 0.24 | 336 ± 33 | 20.4 | 26.2 |
| Small-holder oil palm | 0.34 | 477 ± 22 | 4.7 *4 | 11.6 *4 |
| Commercial oil palm | 0.59 | 827 ± 77 | 2.8 *4 | 7.2 *4 |
| Other | 0.45 *2 | 629 *2 | 2.2 | 2.0 |
| **Relative $E_t$ differences between 1990 and 2011** | – | – | – | **−9 %** |

*1 Average $E_t$ values reported for 12 undisturbed tropical lowland rainforests across the tropics in Kunert et al., 2017; Kume et al., 2011; Lion et al., 2017 and Bruijnzeel, 1990.

*2 Due to the lack of any further information on area type, 'other areas' were assigned the $E_t$ and $E_T$ values of the average of all other land-use types.

*3 Data on extent of undisturbed vs. logged forests from Margono et al., 2012.

*4 Data on extent of commercial vs. small-holder oil palm cultivation from BPS, 2013 (same ratio assumed for 1990 and 2011).

$kg^{-1}$ $H_2O$) than for forest, jungle rubber and rubber systems.

In our study, tree-level measurements were used to estimate stand-level $E_t$. We thus extended our analyses to covariates of mean tree water use *WU* (**Table** S-9). The best predictor for *WU* was the stand structural variable crown projection area per tree ($R^2 > 0.9$), but several further stand structural and productivity-related variables also explained much of the observed variability in *WU* ($R^2 > 0.6$, Table 1**)**. In accordance with the results of our study, close relationships between water use and crown or leaf area related variables, often in contrast to classic stem size related variables such as diameter, have been described in a variety of previous studies (Cermák, 1989; Hatton et al., 1995; Medhurst and Beadle, 2002; Radersma et al., 2006; Alcorn et al., 2013). However, previous studies had to our knowledge never confirmed this across such a large number of study sites and across a land-use trajectory from forest to perennial agricultural monocultures.

So far having discussed the variability across land-use types (n = 32) finally raises the question whether the observed within land-use type variability of $E_t$ (Fig. 2) can be explained. Among the eight forest sites, we found a strong trend of decreasing $E_t$ with increasing $\delta^{15}N$ in the topsoil ($R^2 = 0.86$, $P < 0.001$), which can be interpreted as reduced transpiration with increasing disturbance regime. In jungle rubber stands, $E_t$ rose with increasing water conductive area of the stand ($WCA_{stand}$, $R^2 = 0.52$, $P < 0.05$), which in turn increases with increasing stand density and mean tree diameter. The available datasets further allow for a speculation on the reasons behind very high or low $E_t$ values at single sites. For example, the by far highest $E_t$ at one single jungle rubber site ('BJ6') was particularly due to very high sap flux density ($J_S$). The stand is characterized by fewer but taller and thicker trees and higher structural complexity (laser-scanning based *SSCI*) and leaf area (*PAI*) than at any of the other jungle rubber sites (**Table** S-3). Tree species composition (**Table** S-6) could be a further potential reason for the high observed $J_S$; as such, leaf stomatal conductance and sap flux velocities were found to be much higher in tropical early- than in late-successional tree species (Juhrbandt et al., 2004; Bretfeld et al., 2018). For the monoculture rubber and oil palm plantations, we further found strong effects of age and land-use intensity, which we address in the following section.

The observed strong divergences in covariate performance between the tree- and the stand-level could potentially be due to several reasons. (1) The experimental design of the study was not optimized towards explaining site-to-site variability, but rather towards providing sound mean values for each land-use type. A gradient study design rather than our replicated design likely would have been more successful in identifying underlying ecological drivers of stand-scale $E_t$ (Kreyling et al., 2018). (2) Both our $E_t$ estimate and all potential covariates are associated with estimation uncertainties that may mask underlying relationships at the stand-scale. For assessing $E_t$ at a single site, uncertainties that arise from limited sap flux sampling size may be as high as 30% in the more heterogeneous land-use types forest and jungle rubber (Granier et al., 1996), but likely lower than 15% in the rubber and oil palm monocultures (Niu et al., 2015, 2017). As our study encompassed several replicates per land-use type, uncertainties associated with the overall means are likely substantially lower. However, future studies could benefit from more within-site replicates in heterogeneous land-use types. (3) There might be scaling problems from trees to ecosystem. For scaling our tree level sap flux measurements to stand-level $E_t$, our measurement scheme relies on the key structural variable stand water conductive area. It mainly depends on stand density and mean tree diameter, both of which then form part of the significant multiple linear model. Independent ecosystem-scale measurements of $E_t$, for example via remote sensing, could help to circumvent this problem in future studies. (4) There may be further, unassessed variables such as topographic landscape position or neighborhood effects potentially influencing $E_t$. Still, we found that a high degree of variability in tree-level *WU* was explained by tree structure, and stand-level $E_t$ was largely explained by stand structure and topsoil $\delta^{15}N$. This offers opportunities for a better understanding of the controls of $E_t$ in rapidly changing tropical landscapes.

### 4.3. Influences of plantation age and management

Site-to-site variability in $E_t$ was to 51% (rubber) and 80% (oil palm) explained by plantation age. Over the commonly observed rotation cycles (rubber: 20 years, oil palm: 25 years), $E_t$ was characterized by a rapid increase up to about seven years plantation age (approx. corresponding to canopy closure) and a subsequent steady state for both rubber and oil palm (Fig. 3). Time-averaged $E_t$ over the mentioned rotation cycles was 16% (rubber) and 12% (oil palm) lower (Table 2) than the means at the respective medium-aged core sites (Fig. 2). We found no indications of declining $E_t$ at advanced plantation age for both rubber and oil palm, likely because of the short rotation cycles in these agricultural systems. This stands in contrast to previous studies in even-aged forest stands, which cover much larger time scales per rotation cycle and commonly show, after a relatively early peak, lower $E_t$ with increasing stand age (Jayasuriya et al., 1993; Roberts et al., 2001; Vertessy et al., 2001; Delzon and Loustau, 2005).

In lowland Sumatra, rubber is predominantly grown by smallholders, with no or very little fertilizer input. In contrast, oil palm is grown by smallholders and in commercial, more intensively managed plantations. In two commercial oil palm plantations, $E_t$ was on average 73% higher than in smallholder plantations and 40% higher than at our forest sites (Fig. 3, Table 2). Commercial oil palm $E_t$ was 9% lower than mean $E_t$ in previously studied undisturbed tropical rainforests (Bruijnzeel, 1990; Kume et al., 2011; Kunert et al., 2017; Lion et al., 2017) (Table 2), which is substantial considering e.g. the much lower biomass or leaf area. The substantial sap flux-derived $E_t$ at the commercial oil palm sites is in line with equally substantial evapotranspiration estimates derived from simultaneous eddy covariance measurements at one of the sites (PTPN VI) (Meijide et al., 2017). Reasons for much higher $E_t$ in commercial than in smallholder oil palm plantations are likely related to management intensity. Among our study sites, commercial oil palm plantations received five- to ten-times higher nitrogen fertilization than smallholder plantations (Fan et al., 2015; Teuscher et al., 2016). Although single oil palm smallholder plantations in Indonesia and Jambi, respectively, have been reported to receive much larger amounts of N-fertilizer (up to 170 kg N $ha^{-1}$ $yr^{-1}$, Woittiez et al., 2018) than our smallholder study sites (24–96 kg N $ha^{-1}$ $yr^{-1}$, Fan et al., 2015), averages (141 kg N $ha^{-1}$ $yr^{-1}$, Van Noordwijk et al., 2017) remain substantially below the inputs at our two commercial sites (240–456 kg N $ha^{-1}$ $yr^{-1}$, Fan et al., 2015; Teuscher et al., 2016). Commercial oil palm cultivation also involves more intensive herbicide and pesticide application (Teuscher et al., 2016), as well as optimized harvesting practises and more quality control in the selection of hybrid seedlings used as planting material (Woittiez et al., 2018). Such advanced and more intensive plantation management is associated with substantial increases in oil palm fruit yield (Fan et al., 2015), which is also reflected in higher $E_t$: Among oil palm sites for which approximate data were available (core and commercial sites), we found a linear trend of higher $E_t$ at higher fruit yield (n = 10, $R^2 = 0.34$, $P < 0.05$).

Even though we only had two study sites in commercial oil palm plantations (as opposed to a total of 14 smallholder sites) and the results will thus have to be strengthened further by systematic experimental trials, we found sound indications that agricultural land-use intensification from smallholder to commercial oil palm is accompanied by a substantial increase in $E_t$. To our knowledge, no studies examining in-situ $E_t$ from perennial tropical agricultural crops under different management intensity regimes are available thus far for comparison. However, our results are in line with recent research proposing that increases in productivity of annual crops, or management intensification, increase (evapo)transpiration (Mueller et al., 2016, 2017).

### 4.4. Shifts in transpiration at the local and regional scale

In lowland Sumatra, land-use change is driven by profitability (Clough et al., 2016). In recent years, rubber commodity prices have declined. Together with other socio-economic drivers, this has made oil palm a more attractive land-use option compared to rubber (Kubitza et al., 2018). One main land-use trajectory for a certain unit of land leads from forest degradation over forest conversion to jungle rubber to monoculture rubber plantations to smallholder or commercial oil palm plantations (Clough et al., 2016; Drescher et al., 2016). This linear trajectory results in a U-shaped shift in transpiration, with relatively high $E_t$ in oil palm, particularly in intensively managed commercial plantations (Fig. 4).

Land cover and land use are quite heterogeneous in lowland Sumatra and have changed considerably over time (Clough et al., 2016; Drescher et al., 2016). Oil palm is often more commonly cultivated near larger populated areas with established infrastructure, while rubber often remains the preferred land-use option in remote areas (Euler et al., 2016). In between, some protected forest remnants and other land-use types can be found (Clough et al., 2016; Drescher et al., 2016). At the regional scale, land-use dynamics are thus more complex than depicted in the linear main trajectory for a certain unit of land. Combining stand-level $E_t$ estimates of dominant land-use types from our study with adjusted area fraction estimates for lowland Sumatra (Margono et al., 2012; BPS, 2013; Clough et al., 2016) suggests 9% decreases in regional $E_t$ from 1990 to 2011 (Table 2). Decreases of $E_t$ until 2011 are much more substantial (43%) when taking a time when the forest cover of Sumatra was still largely intact as a baseline for comparison; on the other hand, the predicted continuing conversion to oil palm and particularly land-use intensification to commercial oil palm will likely result in a rebound of regional $E_t$ (**Table** S-1**0**). The latter is in line with recent studies suggesting regionally increasing (evapo)transpiration as a result of cropland expansion and intensification (Betts et al., 2013; Mueller et al., 2016, 2017).

Land-cover change to oil palm and particularly land-use intensification to commercial oil palm plantations can enhance periodical local water scarcity for humans during dry periods (consecutive weeks without precipitation), as has been indicated in interviews with rural villagers (Merten et al., 2016). Soil structure degradation and associated erosion after forest conversion strongly reduce soil water infiltration and increase surface run-off, more so in oil palm plantations than in rubber plantations (Guillaume et al., 2015, 2016; Tarigan et al., 2018). Further, very high canopy interception of precipitation has been reported for oil palm plantations (higher than in forests, Tarigan et al., 2018). In oil palm dominated landscapes, high $E_t$ as reported in our study can lead to additional reductions of available water. In contrast, rubber cultivation seems less concerning in terms of water scarcity for humans due to 30–60% lower $E_t$ (our study), 39% lower canopy interception (Tarigan et al., 2018) and less severe soil degradation (Guillaume et al., 2016).

## 5. Conclusions

We conclude that land-cover change and land-use intensification substantially alter transpiration in lowland Sumatra. Site-to-site variability in $E_t$ is largely explained by stand structural and soil variables and plantation age. Transpiration along a land-use trajectory forest-rubber-oil palm first substantially decreases and then rebounds. We uncovered that particularly commercial, intensive oil palm cultivation leads to very high transpiration. As commercial oil palm cultivation is on the rise in many tropical regions, increases in transpiration due to land-cover change to and intensification in oil palm plantations will become more widespread in the future.

## Declarations of interest

None.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2019.04.017.

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