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Net ecosystem carbon exchange of a dry temperate eucalypt forest

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Abstract. Forest ecosystems play a crucial role in the global carbon cycle by sequestering a considerable fraction of anthropogenic CO₂, thereby contributing to climate change mitigation. However, there is a gap in our understanding about the carbon dynamics of eucalypt (broadleaf evergreen) forests in temperate climates, which might differ from temperate evergreen coniferous or deciduous broadleaved forests given their fundamental differences in physiology, phenology and growth dynamics. To address this gap we undertook a 3-year study (2010–2012) of eddy covariance measurements in a dry temperate eucalypt forest in southeastern Australia. We determined the annual net carbon balance and investigated the temporal (seasonal and inter-annual) variability in and environmental controls of net ecosystem carbon exchange (NEE), gross primary productivity (GPP) and ecosystem respiration (ER). The forest was a large and constant carbon sink throughout the study period, even in winter, with an overall mean NEE of -1234 ± 109 (SE) g C m⁻² yr⁻¹. Estimated annual ER was similar for 2010 and 2011 but decreased in 2012 ranging from 1603 to 1346 g C m⁻² yr⁻¹, whereas GPP showed no significant inter-annual variability, with a mean annual estimate of 2728 ± 39 g C m⁻² yr⁻¹. All ecosystem carbon fluxes had a pronounced seasonality, with GPP being greatest during spring and summer and ER being highest during summer, whereas peaks in NEE occurred in early spring and again in summer. High NEE in spring was

likely caused by a delayed increase in ER due to low temperatures. A strong seasonal pattern in environmental controls of daytime and night-time NEE was revealed. Daytime NEE was equally explained by incoming solar radiation and air temperature, whereas air temperature was the main environmental driver of night-time NEE. The forest experienced unusual above-average annual rainfall during the first 2 years of this 3-year period so that soil water content remained relatively high and the forest was not water limited. Our results show the potential of temperate eucalypt forests to sequester large amounts of carbon when not water limited. However, further studies using bottom-up approaches are needed to validate measurements from the eddy covariance flux tower and to account for a possible underestimation in ER due to advection fluxes.

1 Introduction

Terrestrial ecosystems, together with the ocean, take up more than half of the yearly anthropogenic CO₂ emissions and their combined sink strength has increased over the past 5 decades in step with increased emissions (Ballantyne et al., 2012; Le Quéré et al., 2013, 2015). The terrestrial sink has been mostly attributed to the world's forest ecosystems over the last 2 decades (Le Quéré et al., 2013; Pan et al., 2011)

and only recently has the importance of semi-arid ecosystems in the global carbon sink been identified (Ahlström et al., 2015; Poulter et al., 2014). Even so, forests play a crucial role in the global carbon cycle and climate change mitigation (IPCC, 2013; Pan et al., 2011).

Nonetheless, uncertainty remains regarding the future trend in and strength of this terrestrial carbon sink (Ciais et al., 2013; Mystakidis et al., 2016; Reichstein et al., 2013; Sitch et al., 2015). This is mainly related to the high inter-annual variability in the carbon uptake of ecosystems because of regional and even global variations in climate from year to year (Ahlström et al., 2015; Reichstein et al., 2013). The balance between gross primary productivity (GPP) and ecosystem respiration (ER) – the net ecosystem carbon exchange (NEE) – can be positive (a carbon sink) or negative (a carbon source), although other carbon exchanges such as dissolved organic transport and/or disturbance provide a true net ecosystem carbon balance (NECB) (Chapin et al., 2006). Hence, variability in NEE is dependent on variations in the component fluxes GPP and ER and their responses to climate and resource availability (Ahlström et al., 2015; Ciais et al., 2013; Reichstein et al., 2013). While some studies primarily attribute inter-annual variability in NEE to changes in respiration (Cox et al., 2000; Valentini et al., 2000), others point to a primary dependence on the variability in ecosystem GPP (Ahlström et al., 2015; Jung et al., 2011; Sitch et al., 2015).

Across various ecosystems the main environmental factors controlling GPP have been identified as being solar radiation, water vapour pressure deficit (VPD) and leaf area index (LAI), whereas temperature and soil moisture are the main environmental drivers of ER (Baldocchi, 2008; Beringer et al., 2016; Yi et al., 2010). Variability in NEE has also been demonstrated to be strongly influenced by variation in water availability (i.e. changes in rainfall). For instance, the overall effect of drought conditions has been shown to decrease NEE but it often varies which component, GPP or ER, drought conditions have the greatest impact on (Ciais et al., 2005; Reichstein et al., 2007; Schlesinger et al., 2015; Zhao and Running, 2010). It is therefore critical to assess the carbon balance of ecosystems to improve our knowledge of processes controlling NEE and their response to variability in environmental drivers and climate change. Another factor contributing to the uncertainty of future terrestrial carbon sinks is the still limited empirical data available on forest carbon dynamics to better constrain uncertainties of global and continental process-based carbon models and/or to improve data-driven model frameworks (Haverd et al., 2013a; Jung et al., 2011; Keenan et al., 2012; Roxburgh et al., 2004).

Forests in Australia occupy around 19% of the continent and account for about 3% of forested area worldwide (ABARES, 2013), and until recently their potential contribution to the global carbon cycle had not been considered. The role of Australian ecosystems generally in the global carbon cycle has had recent attention in light of the strong 2011 La Niña event and global record terrestrial car-

bon sink, in which Australian ecosystems, particularly semi-arid ecosystems, played a major role in the continental and global carbon uptake anomaly (Haverd et al., 2013b, 2016; Poulter et al., 2014). Although semi-arid ecosystems have been suggested as dominant drivers in inter-annual variability and trends in the global net carbon sink (Ahlström et al., 2015), little is known about how Australian temperate eucalypt (broadleaved evergreen) forests may contribute to the global sink and inter-annual variability. Two-thirds of native forests in Australia are eucalypt forests (92 Mha) and dry temperate eucalypt forests account for the largest proportion (37% or 8.3 Mha) of forest ecosystems in southeastern and southwestern Australia and are of high socio-economic value (ABARES, 2013). Growth and regeneration of temperate forests in the Northern Hemisphere are considered to account for the increasing global terrestrial carbon sink (Pan et al., 2011), although a recent study showed a decline in this trend (Sitch et al., 2015). While studies of the carbon balance in the Northern Hemisphere temperate forests are abundant, there are only a handful of studies that have been undertaken in temperate eucalypt forests in Australia and none of these were in dry temperate eucalypt forests (Beringer et al., 2016; Keith et al., 2009, 2012; Kilinc et al., 2012, 2013; Leuning et al., 2005; van Gorsel et al., 2013). The behaviour of temperate deciduous broadleaved or evergreen coniferous forests in the Northern Hemisphere cannot be presumed to be an analogue for temperate eucalypt forests. Apart from being broadleaf evergreen, with mostly sclerophyllous leaves, a key trait of eucalypt forests in Australia is the ability to rapidly and opportunistically respond to changing, either favourable or stressful, environmental conditions (Jacobs, 1955; Keith, 1997). This is an adaptation to disturbances such as fire or drought that are a major component of ecosystems on the Australian continent (ABARES, 2013; Beringer et al., 2015; Whitehead and Beadle, 2004). Moreover, Australian forests are generally water and nutrient limited and soils are highly weathered (Attiwill and Adams, 1993; Whitehead and Beadle, 2004). Keith et al. (2009) showed that a wet temperate eucalypt forest had a high carbon uptake capacity compared with other forests globally when not limited by water availability. No studies have been published on ecosystem carbon exchange in dry temperate eucalypt forests, where rainfall is considerably lower and soil moisture is likely to be a greater limiting factor.

The aim of this study was to assess the carbon uptake potential of a dry temperate eucalypt forest and to gain an understanding of its temporal carbon exchange dynamics and controls by using the eddy covariance (EC) technique (Baldocchi, 2008, 2003; Hutley et al., 2005) as part of the regional OzFlux network (Beringer et al., 2016).

Therefore, the objectives of our study were to (1) investigate seasonal and inter-annual variability in NEE, GPP and ER; (2) identify the environmental controls of these CO₂ ecosystem fluxes on seasonal and inter-annual timescales;

and (3) quantify annual estimates of NEE and its component fluxes in a dry temperate eucalypt forest.

2 Materials and methods

2.1 Site description

The Wombat State Forest OzFlux tower site (FLUXNET ID: AUS-Wom) is located in the Wombat State Forest, Victoria, about 120 km west of Melbourne, Australia ($37^{\circ}25'20.5''$ S, $144^{\circ}05'39.1''$ E). The Wombat State Forest is classified as dry sclerophyll eucalypt forest or open (crown cover >50–80%) forest (ABARES, 2013) and is dominated by three broadleaved evergreen tree species: *Eucalyptus obliqua* (L'Hérit.), *Eucalyptus rubida* (Deane & Maiden) and *Eucalyptus radiata* (Sieber ex DC). General forest history includes harvesting and patchy occurrences of bush fires. Selective harvesting occurred until early 1970 when it was replaced by a more intensive shelterwood (two-stage clear felling) system (Poynter, 2005). Since 2003, the Wombat State Forest has been under community forest management, a cooperative between the state government and the local community (Poynter, 2005), and harvesting has been strongly reduced. Forest management practices also include periodic low-fire-intensity prescribed fires and firewood collection in designated areas.

The study site is a secondary regrowth forest (DSE, 2012), of mixed age, with an average canopy height of 22 m (Griebel et al., 2015), a basal area of $37 \text{ m}^2 \text{ ha}^{-1}$ (Moore, 2011) and an LAI of 1.8 (Griebel et al., 2016; Moore, 2011). The area was last selectively harvested in the early 1970s with the last bush fire on the outskirts of the study site recorded in 1982 and no recorded history of prescribed fires. The flux tower is located on a ridge at a mean altitude of 706 m a.s.l. and the terrain within the footprint is relatively level to the east of the tower, with gently sloping gullies ($<8^{\circ}$) towards the southwest and northwest (Griebel et al., 2016). The understorey is sparse and dominated by austral bracken (*Pteridium esculentum* (G. Forst.) Cockayne), forest wire-grass (*Tetrarrhena juncea* R. Br.), tussock grass (*Poa sieberiana* Sprengel), herbs (e.g. *Gonocarpus tetragynus* Labill., *Viola hederacea* Labill.) and rushes (*Lomandra* spp.) (Tolhurst, 2003). The climate is cool temperate to Mediterranean with wet, cold winters and dry, warm and hot summers. Long-term (2001–2013) mean annual air temperature was $12.1 \pm 0.1^{\circ}\text{C}$, with mean monthly maximum air temperatures of $26.3 \pm 0.5^{\circ}\text{C}$ in January and mean minimum air temperatures of $3.2 \pm 0.1^{\circ}\text{C}$ in July (nearest Bureau of Meteorology (BoM) station Ballarat, 28 km SW; Fig. 1a). The silty clay soil overlies clay derived from Ordovician marine sediments and is classified as acidic-mottled, dystrophic, yellow Dermosol (Robinson et al., 2003), which is moderate to highly weathered and exhibits low fertility. The long-term (1901–2014) mean annual rainfall at the nearest rainfall BoM station (Daylesford,

11 km N; Fig. 1b) is $879 \pm 18 \text{ mm}$, with the highest rainfall occurring during winter and spring. For an overview and more detailed site characteristics, see Table 1.

2.2 Instrumentation and data acquisition

The guyed EC flux tower was established in January 2010 within a fenced compound. The micro-meteorological measurement system was installed at 30 m height and consisted of an open-path infrared gas analyser (IRGA; Li-7500, LI-COR, Lincoln, USA) that measures CO_2 , water vapour concentrations, and atmospheric pressure and a 3-D sonic anemometer (CSAT3, Campbell Scientific Inc., Logan, USA) that measures turbulent wind vectors and virtual air temperature. Instantaneous measurements were carried out at 10 Hz and were stored on a CF (compact flash) card. Furthermore, calculated covariances with a 30 min averaging period were stored on a data logger (CR-3000, Campbell Scientific Inc., Logan, USA). Prior to the calculation of covariances at the end of a 30 min averaging period, 10 Hz data were filtered by the data logger depending on diagnostic information from both the sonic anemometer and IRGA in which data spikes were removed (Isaac et al., 2017). Concurrent measurements of environmental variables included air temperature (T_a) and absolute and relative humidity (HMP-45C probe, Vaisala, Finland) at 2 and 30 m height, incoming and reflected short-wave radiation and atmospheric and surface-emitted long-wave radiation measured with a CNR1 net radiometer (Kipp and Zonen, Delft, the Netherlands) at 30 m height, rainfall measured with a tipping bucket rain gauge (CS702, Hydrological Services Pty Ltd., Sydney, Australia) at 1 m height, soil heat flux averaged over two sites at 8 cm depth (HFT3 plate, Campbell Scientific Inc., Logan, USA, and HFP01 plate, Hukseflux, Delft, the Netherlands), soil temperature (T_s) averaged over two sites at 10 cm depth (TCAV Thermocouple probes, Campbell Scientific Inc., Logan, USA), and volumetric soil water content (SWC) at 10 cm (averaged over two sites) and 50 cm depth (CS616 water content reflectometer probes, Campbell Scientific Inc., Logan, USA). All instrumentation was powered by a remote area power system consisting of a diesel generator and a 24 V battery bank inverter system (Powermaker Ranger 4.5, Eniqwest, Australia). An automated remote connection using a GSM modem (GPRS/GSM Quadband Unimax router and Ethernet modem, Maxon Australia Pty Ltd., Padstow, Australia) provided real-time information on system status and ensured data acquisition on a daily basis. Additionally, data were stored on external CF cards, which were interchanged on a monthly basis. A footprint analysis by Griebel et al. (2016) using the parameterization of flux footprint predictions of Kljun et al. (2004) showed that the distribution of fluxes was relatively homogeneous and that the whole footprint consisted of the same forest type and dominant tree species and a roughly uniform basal area. For further details, see Griebel et al. (2016).

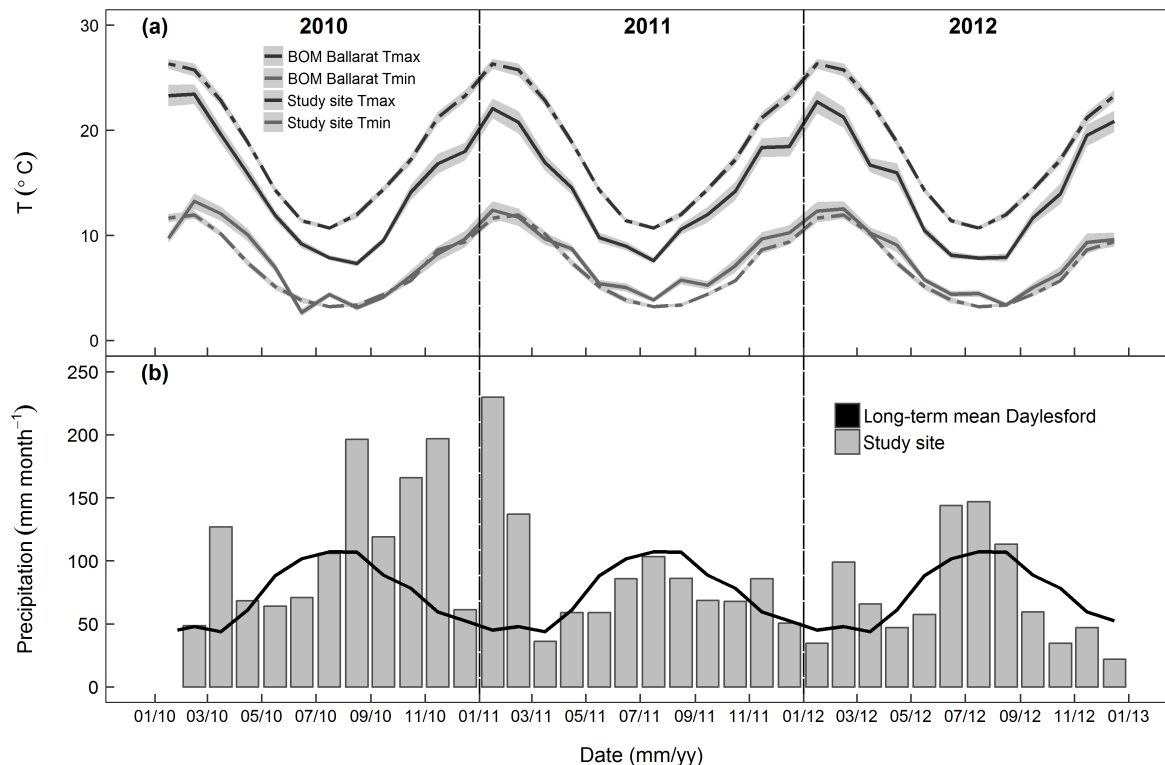


Figure 1. Climate time series of (a) monthly averages of minimum (grey lines) and maximum (black lines) air temperatures from the study site from 2010 to 2012 (solid lines) and from the BoM station Ballarat from 2001 to 2013 (dashed lines); shaded areas indicate ± 1 SE. (b) Monthly rainfall at the Wombat State Forest OzFlux EC tower site from 2010 to 2012 (grey bars) and 114-year (1901–2014) long-term monthly mean rainfall at the BoM station Daylesford (black line).

Table 1. Site and tower characteristics for the Wombat State Forest OzFlux site.

| | |
|--------------------------------------------------------|--------------------------------------------------------------------------------------------------------|
| Location | 37°25' S, 144°05' E |
| Elevation a.s.l. (m) | 706 |
| Forest size (ha) | 70 000 |
| Tower height (m) | 30 |
| Canopy height (m) | 22 ^b |
| Canopy species | <i>Eucalyptus obliqua</i> , <i>E. rubida</i> , <i>E. radiata</i> |
| Understorey species | <i>Pteridium esculentum</i> , <i>Tetrarrhena juncea</i> , <i>Poa sieberiana</i> , <i>Lomandra</i> spp. |
| Mean annual air temperature (°C) | 11.0 \pm 0.1 |
| Mean annual rainfall (114 years, mm) ^a | 879 \pm 18 |
| LAI (leaf area index, m ² m ⁻²) | 1.81 ^c |
| Tree density (ha ⁻¹) | 1316 ^c |
| Tree dbh ^d (cm) | 18.6 ^c |
| Litterfall (g m ⁻² yr ⁻¹) | 1120 \pm 52 |
| Soil type | acidic-mottled, dystrophic, yellow Dermosol |
| Soil depth (cm) | 50 cm |
| pH | 4.83 \pm 0.02 |
| Bulk density (0–10 cm, kg m ⁻³) | 0.94 \pm 0.02 |
| C/N | 30.9 \pm 0.5 |
| Sand (%) | 45.4 \pm 1.8 |
| Silt (%) | 27.9 \pm 1.9 |
| Clay (%) | 26.7 \pm 0.4 |

Where applicable: mean of $n = 3 \pm 1$ SE. ^a BoM station Daylesford, 11 km N of study site). ^b Griebel et al. (2015). ^c Moore (2011). ^d Dbh: diameter at breast height.

In February 2012, a custom-built profile system including an IRGA (Li-840, LI-COR, Lincoln, USA) and six vertical layers (1, 2, 4, 8, 15 and 30 m) was installed to measure CO₂ concentrations of each layer in 2 min intervals (McHugh et al., 2017). A detailed description of the profile system can be found in McHugh et al. (2017). Due to technical problems with the IRGA profile, data were available from March to October 2012. Changes in the storage term between the forest floor and EC measurement point were calculated following McHugh et al. (2017) and Finnigan (2006). For periods of time when profile storage measurements were not available, ecosystem CO₂ fluxes were accounted for by storage terms derived from single-point calculations within the OzFluxQC data processing (Isaac et al., 2017). However, the contribution of storage term only marginally changed the magnitude of NEE (on average 2 %) (Fig. S1 in the Supplement).

2.3 Data processing

2.3.1 Quality control

Quality assurance and quality control (QA–QC) and eddy covariance flux corrections were performed on both available 10 Hz data and 30 min covariance data. The 10 Hz data were processed with EddyPro version 6.2 (EddyPro, 2016), including default statistical analysis (spike removal, dropouts, absolute limits, skewness and/or kurtosis), low- and high-frequency correction (Massman, 2000; Moncrieff et al., 2005), and planar-fit coordinate rotation (Wilczak et al., 2001). The calculated covariances from the 30 min averaging period were processed following the OzFlux standard protocol and open source code OzFluxQC version 2.9.6e (Isaac et al., 2017, 2016) using Anaconda Python version 2.7 (Continuum Analytics, Texas, USA). The procedure is described in detail in its own method paper by Isaac et al. (2017), as well as by Eamus et al. (2013) and Cleverly et al. (2013). In brief, the OzFluxQC procedure included quality control checks such as range checks in plausible limits, spike detection, dependency checks and manual rejection of date ranges of all measured variables (covariances and environmental variables) depending on site characteristics and based on visual revision of the data during the QA–QC procedure modified per month and year: linear corrections for calibration anomalies and sensor drift, 2-D coordinate rotation (Lee et al., 2005), Webb–Pearman–Leuning correction (Webb et al., 1980), low- and high-frequency correction according to Massman (2001, 2000) and Moncrieff et al. (2005), conversion of virtual heat flux to sensible heat flux and correction of ground heat flux for heat storage in the soil layer above, addition of single-point-calculated or profile-measurement-derived storage term, and calculation of fluxes from the quality-controlled and corrected covariances. Extensive comparison between 10 Hz data processed with EddyPro and 30 min covariances processed with OzFluxQC showed that the planar-fit correction versus 2-D-coordinate rotation re-

sulted in a 3 % difference of fluxes. When this difference was accounted for in the OzFluxQC processed data set, both data sets were in very good agreement (slope: 1.01, intercept: 0.06, R^2 : 0.90). Periods of data with low turbulence conditions, predominantly during night-time, were excluded based on friction velocity (u^*). Night-time u^* was filtered with yearly determined u^* thresholds using the change-point detection (CPD) method after Barr et al. (2013) and is described in detail in Isaac et al. (2017), Beringer et al. (2017) and McHugh et al. (2017), this issue. Uncertainty in the u^* threshold was estimated by generating a probability distribution for the u^* threshold and 95 % confidence interval (CI) by bootstrapping the CPD method (1000 times randomly sampling of the data per year). Annual u^* thresholds ranged from 0.53 to 0.66 m s⁻¹. Data gaps occurred due to rainfall and occasional power failure and 60 % of data were available over the 3-year period. Following QA–QC and night-time u^* filtering, this was reduced to 37, 49 and 49 % in 2010, 2011 and 2012. From these values, quality-filtered data were 64 % daytime data and 26 % night-time data.

2.3.2 Gap filling

Subsequent gap filling of data was done either with the Dynamic INtegrated Gap-filling and partitioning for OzFlux (DINGO v13) routine (Beringer et al., 2017) or with the OzFluxQC procedure (Isaac et al., 2017), depending on the partitioning method selected (see below). However, both procedures have very similar data gap-filling procedures and are described in detail in Beringer et al. (2017) and Isaac et al. (2017). Small data gaps (≤ 2 h) of continuous 30 min flux measurements and environmental variables were filled with linear interpolation.

In DINGO, data gaps of environmental variables (air temperature, humidity, radiation, wind speed, atmospheric pressure and rainfall) >2 h were gap filled: (1) from linear regressions with AWS (automated weather station) 30 min data records from the three nearest BoM weather stations, which were ranked after best correlation and (2) with spatially gridded meteorological daily satellite data at 0.1° resolution from the Australian Water Availability Project (AWAP; Raupach et al., 2009). In the unlikely event that gaps were still present after applying the methods above, then monthly diurnal means of measured climate variables were used. The frequency at which the correlation analysis between flux tower data and AWS was performed was set to use all available data. Soil temperature and soil moisture variables were gap filled using a simulation of the land surface using AWAP climate data and the CSIRO process-based land surface model BIOS2 at 0.05° resolution (see Haverd et al., 2013a) adjusted to site observations. Following gap filling of environmental variables, half-hourly NEE data were gap filled using a feed forward artificial neural network (FFNET) with incoming shortwave solar radiation (F_{sd}), vapour pressure deficit (VPD), SWC, T_s , wind speed (WS) and enhanced vegetation index (EVI)

as input drivers according to Beringer et al. (2007, 2017) and Papale and Valentini (2003). EVI was obtained from 16-day compositing periods from MODIS (Moderate Resolution Imaging Spectroradiometer; see Huete et al., 2002) as surrogate information of vegetation activity (i.e. LAI and growth) and interpolated to 30 min as a proxy for production related to plant respiration. Frequency of gap filling using a neural network (NN) was set to all available data.

In OzFluxQC, data gaps of environmental variables > 2 h were gap filled: (1) with AWS as in DINGO, (2) using the regional Australian Community Climate Earth System 5 Simulator (ACCESS-R) numerical weather prediction (NWP) model at a resolution of 12.5 km run by the BoM (Isaac et al., 2017) and (3) ERA-Interim (ERA-I) data set from the European Centre for Medium Range Weather Forecasting (Dee et al., 2011) at 75 km resolution across Australia. Half-hourly NEE data were gap filled using the SOLO NN (Abramowitz, 2005; Hsu et al., 2002) with net radiation (F_n), ground heat flux (F_g), specific humidity (q), VPD, SWC, T_a and T_s as input drivers according to Isaac et al. (2017).

2.3.3 Partitioning and carbon flux definitions

The partitioning of NEE into its component fluxes GPP and ER was following the assumption of

$$NEE = ER - GPP, \quad (1)$$

in which daytime NEE is the difference of GPP and ER, and night-time NEE is equal to ER. Hence, GPP is negligible or zero. We adopt the conventions in Chapin et al. (2006) in which GPP and ER fluxes are designated with a positive sign. Negative NEE fluxes denote a net carbon flux from the atmosphere to the ecosystem and thus a net carbon uptake by the forest ecosystem.

One of the most common uncertainties in EC measurements can be an underestimation of night-time NEE or ER as turbulent mixing is often lower or absent at night-time, which can lead to undetectable vertical and horizontal advection of CO_2 within the canopy (Aubinet et al., 2012; Baldocchi, 2003; Goulden et al., 1996; van Gorsel et al., 2007). Although u^* filtering is the most common correction for this underestimation error (Goulden et al., 1996), many studies have reported smaller estimates of ER from u^* -filtered and gap-filled EC tower data compared to those from chamber measurements of soil, leaf and stem respiration (Keith et al., 2009; Lavigne et al., 1997; Law et al., 1999; Phillips et al., 2010; Speckman et al., 2015). Although no independent upscaled ER estimates from chamber measurements were available from our study site, we used independent daily soil respiration data from a separate study at the same study site (Hinko-Najera, 2016, unpublished data) to visually compare its relative contribution to daily tower ER estimates derived from four different data selection and subsequent partitioning methods to reduce a potential underestimation of ER (see Supplement Figs. S1, S2 and

S3). We ran an ensemble of different partitioning methods (using either DINGO or OzFluxQC routines) and u^* -based night-time filters on NEE fluxes, including only the storage term, to evaluate variation in ecosystem carbon fluxes depending on the partitioning and filter method used. An overview of partitioning methods, estimated annual sums and their variation is given in the Supplement in Tables S1, S2 and Fig. S4 and briefly explained here. We used three different partitioning methods to estimate gross ecosystem carbon fluxes: (1) the night-time approach after the Lloyd and Taylor temperature-response function (Lloyd and Taylor, 1994; Reichstein et al., 2005) with T_a as the input driver using a window size of 15 days with an overlapping of 10 days in OzFluxQC; (2) night-time approach using the NN: (2a) FFNET with T_s , T_a , SWC and EVI as input drivers and a window size of all available data in DINGO (Beringer et al., 2017) or (2b) SOLO NN with T_a , T_s and SWC as input drives and a window size of 1 year in OzFluxQC (2b) (Isaac et al., 2017); and (3) the daytime approach using the light-response function according to Lasslop et al. (2010) using either (3a) DINGO or (3b) OzFluxQC with a window size of 15 days with an overlapping of 10 days. Detailed descriptions of functions and routines used within the DINGO and OzFluxQC routines are given in Beringer et al. (2017) and Isaac et al. (2017). For the methods using the night-time approach, the u^* filter after the u^* threshold was applied to non-gap-filled (quality-controlled observations only) night-time ($F_{sd} < 10 \text{ W m}^{-2}$) NEE flux data. The differences between DINGO (2a) and OzFluxQC (1, 2b) partitioning methods here is that DINGO was set to use u^* -filtered night-time data from the first 3 hours after sunset only ($F_{sd} < 10 \text{ W m}^{-2}$) while with OzFluxQC three night-time selections have been applied to u^* -filtered night-time data: all u^* filtered night-time NEE data, first three hours after sunset of u^* filtered NEE data, and a variable daily window size using all night-time data above the u^* threshold from sunset onwards until u^* fall below the u^* threshold (Eva van Gorsel, personal communication). The selection of the first 3 hours after sunset is based on an extensive study in a wet temperate eucalypt forest from van Gorsel et al. (2008, 2007), who demonstrated that ER was at a maximum in the early evening hours when the canopy is still coupled with the atmosphere. For the NN methods (2a) and (2b), estimated night-time ER was extrapolated to daytime ER. The final NEE flux was then constructed from gap-filled daytime data ($F_{sd} \geq 10 \text{ W m}^{-2}$) and estimated ER at night-time. GPP was then subsequently estimated with Eq. (1). For the methods using the daytime approach, a light-response curve (LRC) was fitted to daytime NEE to estimate GPP and subsequently ER across day and night.

2.4 Uncertainty analysis and analysis of environmental drivers

We performed an uncertainty analysis as described in McHugh et al. (2017), which includes an uncertainty estimation of combined random and model error (Hollinger and Richardson, 2005; Keith et al., 2009) (Supplement Table S3) and the effect of uncertainties in u^* thresholds on annual NEE estimates by using the lower (5 %) and upper (95 %) confidence interval of the probability distribution of the mean u^* threshold (Barr et al., 2013) (Supplement Table S4). The uncertainty introduced due to random (measurement) and model error was small for 2010 and 2012 (4 and 6 % of annual NEE estimate) and slightly higher for 2011 (10 % of annual NEE estimate) (Table S3). Estimations of the uncertainties in u^* thresholds on annual NEE were small for the lower u^* uncertainty bound (5 % CI), ranging from $-19 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2012 to $26 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2011 (1–2 % of annual NEE estimate). We could not estimate an upper u^* uncertainty bound (95 % CI) as data availability was insufficient (Table S4).

To analyse environmental controls (F_{sd} , T_{a} , VPD and SWC) on the seasonal and inter-annual variability in daytime NEE, a rectangular hyperbolic LRC or Michaelis–Menten equation (Carrara et al., 2004; Falge et al., 2001; Flanagan et al., 2002; Lasslop et al., 2010; Michaelis and Menten, 1913) was used to determine the dependency of daily means of quality controlled half-hourly non-gap-filled midday NEE (hours 11:00–13:00 AEST) on F_{sd} :

$$\text{NEE}_{\text{midday}} = \frac{\alpha \times F_{\text{sd}} \times \beta}{\alpha \times F_{\text{sd}} + \beta}, \quad (2)$$

in which F_{sd} is the incoming solar radiation (W m^{-2}), α is the slope of LRC or the canopy light utilization efficiency ($\mu\text{mol CO}_2 \text{ J}^{-1}$) and β is the maximum NEE or uptake rate of the canopy at light saturation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Residuals of the LRC were then used to analyse the dependency of midday NEE on either T_{a} or VPD (given the strong correlation between VPD on T_{a}) (Carrara et al., 2004; Chen et al., 2002) with linear and non-linear regressions, i.e. exponential temperature sensitivity functions according to Lloyd and Taylor (1994) for T_{a} (see Eq. 3 below) and a logarithmic power model according to Chen et al. (2002) for VPD. However, for both T_{a} and VPD, linear relationships resulted in the best fits, whereas non-linear regressions consistently resulted in arbitrary or insignificant parameter estimates. The influence of SWC on daytime NEE was tested with linear regressions between SWC and residuals of LRC. Second residuals from the linear relationships between LRC residuals and T_{a} as temperature and soil moisture are often negatively correlated in this forest ecosystem (Hinko-Najera et al., 2015). To analyse the effect of T_{a} , VPD and SWC on LRC, data were divided into T_{a} , VPD and SWC bins.

For the analysis of environmental controls (T_{a} , SWC) on the seasonal and inter-annual variability in night-time NEE,

an Arrhenius-type model function (LT) according to Lloyd and Taylor (1994) was applied to determine the temperature sensitivity of daily means of half-hourly quality-controlled non-gap-filled and u^* -filtered night-time NEE:

$$\text{NEE}_{\text{NT}} = R_{\text{ref}} \times \exp\left(E \times \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_{\text{a}} - T_0}\right)\right), \quad (3)$$

in which R_{ref} is the basal respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at the reference air temperature of 10°C ($T_{\text{ref}} = 283.15 \text{ K}$), E the activation energy parameter, T_0 a fixed temperature parameter ($T_0 = 227.13 \text{ K}$) according to Lloyd and Taylor (1994), and T_{a} the air temperature (K). Residuals of LT were then used to analyse the dependency of night-time NEE on SWC with linear regressions. To analyse the effect of SWC on LT, data were divided into SWC bins.

All subsequent data manipulation and statistical analyses were done using R version 3.3.2 (R Core Team, 2016), and for gap-filled times series we chose the night-time partitioning approach from the DINGO output. Differences in seasonal and inter-annual variations in daily means were tested with the Kruskal–Wallis rank sum test and Dunn’s test.

3 Results

3.1 Seasonal and inter-annual variation in environmental variables

Seasonal and inter-annual patterns in rainfall varied markedly across the 3-year period (Figs. 1b, 2f). In the first 2 years unusually high rainfall was observed during the occurrence of two strong La Niña events. Annual rainfall in 2010 and 2011 was 43 and 22 % above the long-term mean annual rainfall from the nearest BoM station (Daylesford), which is representative for the study site as an adjustment was less than 1 % (Tables 1, 2). Most of the anomalous rainfall occurred between August 2010 and February 2011, with a 2-fold increase in rainfall during spring 2010 (SON) and a 3-fold increase in rainfall in summer 2010/11 (DJF, Fig. 1b). While the annual rainfall in 2012 was close to the long-term mean annual rainfall (Tables 1, 2), monthly rainfall showed a distinct pattern with the long-term mean rainfall in February 2012 (2-fold increase) above and winter 2012 (JJA, +30 %) but below long-term mean rainfall from spring 2012 (SON, –37 %) onwards (Figs. 1b, 2f).

SWC at 10 cm soil depth generally varied strongly with seasons and was highest during winter, with a daily maximum of $0.36 \text{ cm}^3 \text{ cm}^{-3}$ observed in August 2012, and decreased towards summer, reaching a daily minimum of $0.12 \text{ cm}^3 \text{ cm}^{-3}$ in February 2012 (Fig. 2e). Seasonal variability in SWC was more pronounced in 2012 (CV = 25 %) than in 2010 (CV = 18 %) as high rainfall led to an absence of a dry period during summer 2010/11 (DJF) and SWC remained relatively stable and high throughout 2011 (CV = 13 %).

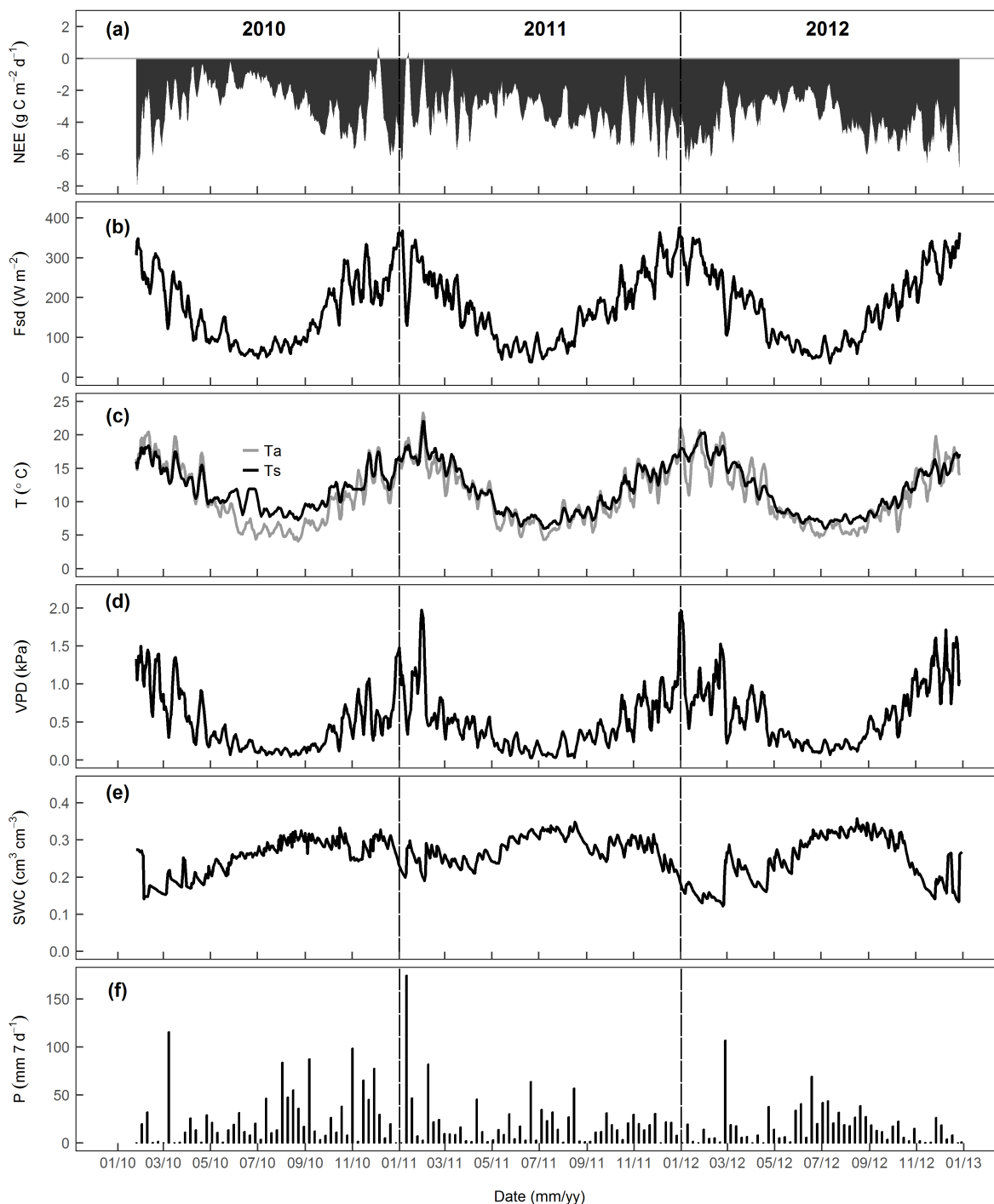


Figure 2. Time series of (a) 7-day running means of daily total net ecosystem exchange (NEE), 7-day running means of daily averages of (b) incoming solar radiation (F_{sd}), (c) air (T_a) and soil (T_s) temperature, and (d) 7-day running means of mean midday (11:00–13:00 AEST) vapour pressure deficit (VPD), (e) daily averages of volumetric soil water content (SWC), and (f) 7-day sums of rainfall (P) from 2010 to 2012.

F_{sd} , T_a , T_s and VPD showed a strong seasonality, with maximum values during summer months and minimum values during winter months (Fig. 2b, c, d). Mean daily F_{sd} was 278 W m^{-2} in summer (maximum of 411 W m^{-2} in Jan-

uary 2011) and 81 W m^{-2} in winter (minimum of 5 W m^{-2} in May 2011; Fig 2b). Daily mean temperatures ranged from 2.0°C in winter (JJA) to 28.2°C in summer (DJF) for T_a and from 4.8 to 23.6°C for T_s (Fig. 2c). A daily maxi-

Table 2. Annual averages of incoming solar radiation (F_{sd}), air temperature (T_a), soil temperature (T_s), soil water content (SWC), vapour pressure deficit (VPD), annual sums of rainfall (P), net ecosystem exchange (NEE), ecosystem respiration (ER) and gross primary productivity (GPP) at Wombat State Forest from 2010 to 2012; CV – coefficient of variation for inter-annual variation; inter-annual differences are indicated with *** ($p < 0.001$), ** ($p < 0.01$) or ns (not significant). Letters indicate year-to-year differences.

| Year | F_{sd} (W m^{-2}) | T_a ($^{\circ}\text{C}$) | T_s ($^{\circ}\text{C}$) | SWC (v/v) | VPD (kPa) | P (mm) | NEE (g C m^{-2}) | ER (g C m^{-2}) | GPP (g C m^{-2}) |
|--------|-----------------------------------|---------------------------------|---------------------------------|------------------|--------------|-------------|--------------------------------|-------------------------------|--------------------------------|
| 2010* | 174 | 11.0 | 12.1 | 0.25 a | 0.36 a | 1254 | −1046 a | 1603 a | 2649 |
| 2011 | 177 | 11.1 | 11.8 | 0.27 b | 0.32 a | 1070 | −1231 b | 1534 a | 2764 |
| 2012 | 182 | 11.1 | 11.8 | 0.24 a | 0.47 b | 872 | −1424 c | 1346 b | 2770 |
| CV (%) | 2.5 ns | 0.5 ns | 1.2 ns | 6.6*** | 20.0*** | 17.9 | 15.3*** | 8.9*** | 2.5 ns |

* Includes extrapolated values until 21 January; estimates without extrapolation, i.e. 344 days: P (mm): 1229, NEE (g C m^{-2}): −958, ER (g C m^{-2}): 1476, GPP (g C m^{-2}): 2434.

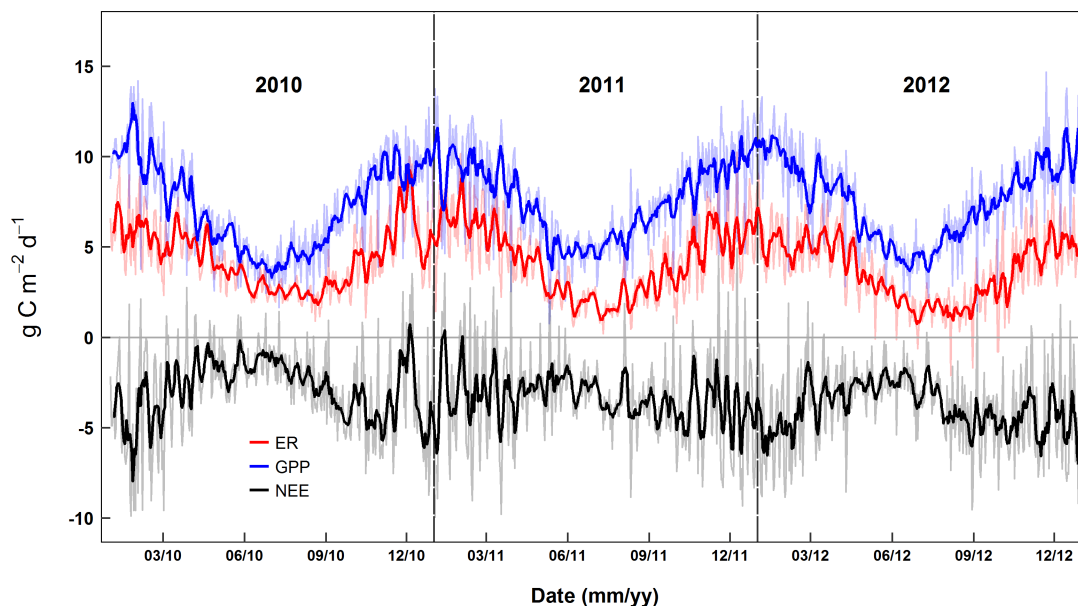


Figure 3. Ecosystem carbon fluxes of the Wombat State forest OzFlux site from 2010 to 2012: ecosystem respiration (ER, red lines), gross primary productivity (GPP, blue lines) and net ecosystem carbon exchange (NEE, black lines). Displayed is the output of the DINGO partitioning method (2a) using the night-time data approach with NN and early evening hours with daily totals ($\text{g C m}^{-2} \text{d}^{-1}$) of ecosystem carbon fluxes (shaded lines) and 7-day running means of daily totals (bold lines) for better illustration.

mum midday VPD of 3.41 kPa was observed in January 2012 (Fig. 2d). Inter-annual variation in F_{sd} , T_a and T_s was marginal (Fig. 2b, c), while mean annual VPD was significantly ($p < 0.001$) higher in 2012 (0.47 kPa) compared to 2010 and 2011 (0.36 and 0.32 kPa; Table 2).

3.2 Seasonal and inter-annual variation in CO_2 ecosystem fluxes

A pronounced seasonal pattern was observed in ER (CV = 39 %) but less so in GPP (CV = 27 %) and NEE (CV = 24 %; Figs. 2a, 3, 4).

In general, the forest showed near-continuous net carbon uptake (negative NEE) throughout the 3-year pe-

riod, with the highest net uptake rates during summer and spring months (seasonal daily means of NEE: -4.07 and $-3.98 \text{ g C m}^{-2} \text{d}^{-1}$) and the lowest rates during winter and autumn (seasonal daily mean NEE: -2.86 and $-2.62 \text{ g C m}^{-2} \text{d}^{-1}$; Figs. 2a, 3). Only in December 2010 and January 2011, did NEE become distinctly positive (net carbon loss) for a short period (3 to 4 consecutive days) due to an increase in ER in December 2010 and a decrease in GPP in January 2011 (by $\sim 40\%$) in response to considerably high rainfall and limited solar input. Seasonal variability in NEE was noticeably less pronounced in 2011 (CV = 9 %) than in 2010 ($p < 0.001$, CV = 38 %) and 2012 ($p < 0.001$, CV = 21 %; Fig. 4a). Inter-annual variation in NEE was high

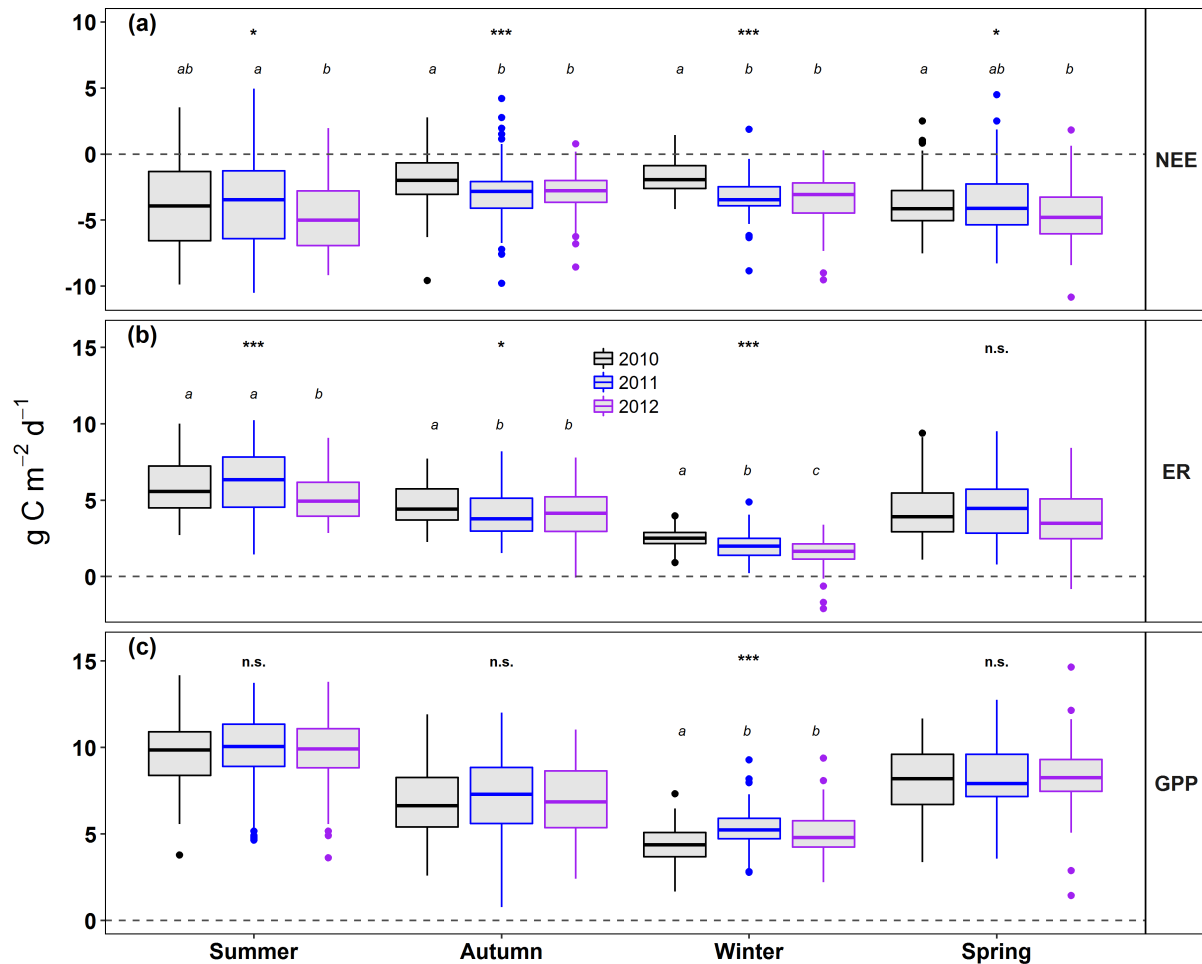


Figure 4. Box-and-whisker plots of daily averages of (a) NEE, (b) ER and (c) GPP for years and seasons; inter-annual differences are displayed for each season with p values (significance level $p < 0.05$); letters indicate year-to-year differences.

(CV = 15 %) and significant ($p < 0.001$) with most evident differences during winter and autumn (Table 2, Fig. 4a).

ER was greatest during summer (seasonal daily mean of $5.77 \text{ g C m}^{-2} \text{ d}^{-1}$), of similar magnitude in autumn and spring (4.34 and $4.23 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively), and lowest during winter ($2.05 \text{ g C m}^{-2} \text{ d}^{-1}$). Similar to NEE, GPP was greatest during summer (seasonal daily mean of $9.85 \text{ g C m}^{-2} \text{ d}^{-1}$), followed by spring ($8.20 \text{ g C m}^{-2} \text{ d}^{-1}$), autumn ($6.96 \text{ g C m}^{-2} \text{ d}^{-1}$), and winter ($4.91 \text{ g C m}^{-2} \text{ d}^{-1}$).

Overall inter-annual variation in ER was moderate (CV = 9 %) and significant for all seasons except spring. ER was significantly lower in summer 2012 compared to the summer months in 2010 and 2011, as was winter 2012 compared to winters 2010 and 2011 (Fig. 4b). Overall, GPP estimates did not vary between years (CV < 3 %), and only in winter 2010 did GPP significantly differ from the winters of 2011 and 2012 (Fig. 4c). The ER / GPP ratio was highest during autumn and summer (0.62 and 0.59) and lowest during spring and winter (0.52 and 0.42).

3.3 Environmental drivers of CO_2 ecosystem fluxes

Results of the LRC fits and linear fits with T_a and VPD per year and season are presented in Table 3. Overall, F_{sd} explained 25 % of the temporal variability in midday NEE (Fig. 5a), which did not considerably vary between observation years. Similarly, both T_a and VPD explained about 18 or 23 % of the overall temporal variability in midday NEE (Fig. 5b, c), and again no considerable inter-annual differences were determined. However, a clear distinct seasonal pattern was shown in the dependence of midday NEE on F_{sd} , T_a and VPD when coefficients of determinations were plotted for each month (Fig. 6a). While F_{sd} was the dominant environmental driver during the mid- to late autumn and winter months (36–47 %, mean = 42 %), T_a and VPD were the main controlling environmental variables during the spring, summer and early autumn months (23–56 %, mean = 40 % for T_a and 15–48 %, mean = 31 % for VPD). LRCs fitted for various T_a bins and VPD bins (Table 4) show a strong decrease in the net carbon uptake at temperatures above 20°C or VPD

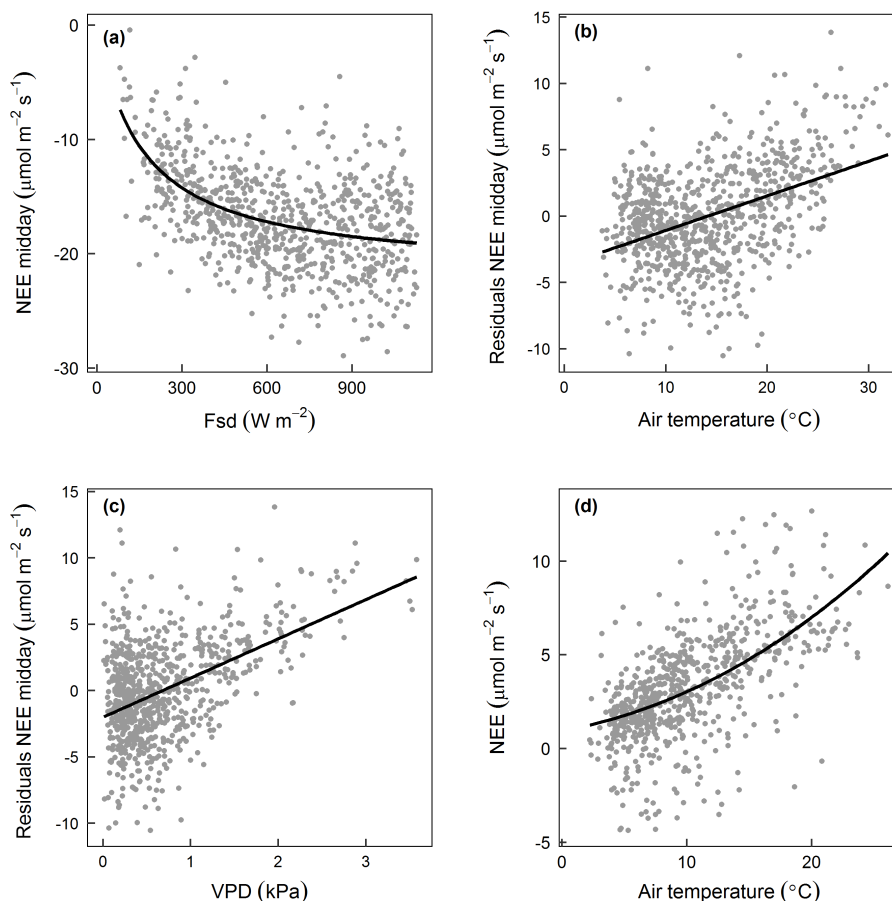


Figure 5. (a–c) Relationship between daily means of midday NEE and (a) incoming solar radiation (F_{sd}) as a rectangular hyperbolic light-response curve (LRC), linear fits between residuals of LRC and (b) air temperature (T_a) or (c) vapour pressure deficit (VPD). (d) Relationship between daily means of u^* -filtered night-time NEE and air temperature (T_a) as a temperature-response function after Lloyd and Taylor (1994); R^2 values are given in Tables 3 and 5.

Table 3. Parameters, standard errors and/or the coefficient of determination (R^2) of (a) the rectangular hyperbolic light-response curve (LRC) between daily means of midday NEE and incoming radiation (F_{sd}), (b) linear fits between residuals of LRC and air temperature (T_a) or vapour pressure deficit (VPD), and (c) linear fits between second residuals (b) with T_a and soil water content (SWC) for subsets of data. α : initial slope of LRC and canopy light-utilization efficiency ($\mu\text{mol CO}_2 \text{ J}^{-1}$); β : maximum NEE (i.e. uptake rate of the canopy) at light saturation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Significance level: *** < 0.001, ** < 0.01, * < 0.5; ns: not significant. nr: number of data points.

| Data subset | (a) F_{sd} | | | (b) T_a | VPD | (c) SWC | nr |
|-------------|-----------------|----------------|-------|-----------|---------|---------|-----|
| | α (SE) | β (SE) | R^2 | R^2 | R^2 | R^2 | |
| All data | -0.14 (0.01)*** | -21.8 (0.0)*** | 0.25 | 0.18*** | 0.23*** | 0.05*** | 792 |
| 2010 | -0.11 (0.02)*** | -22.5 (0.0)*** | 0.28 | 0.19*** | 0.25*** | 0.05*** | 213 |
| 2011 | -0.13 (0.02)*** | -21.9 (0.0)*** | 0.27 | 0.21*** | 0.21*** | 0.10*** | 292 |
| 2012 | -0.17 (0.02)*** | -21.3 (0.0)*** | 0.22 | 0.15*** | 0.24*** | 0.04*** | 287 |

values above 1.2 kPa. A clear differentiation between T_a and VPD was very difficult because of the strong correlation between VPD and T_a . While overall and inter-annual variability in residuals of midday NEE were marginally better explained by VPD than T_a , variability in midday NEE residuals from spring to early autumn correlated more strongly with changes

in T_a than VPD. No apparent influence of SWC on residuals of NEE or LRCs was determined (Tables 3c, 4).

Results of LT and linear fits with SWC per year and season are presented in Table 5. Overall, 36 % of the temporal variability in u^* -filtered night-time NEE was explained by T_a (Fig. 5d), which varied from 30 % in 2012 to 31 %

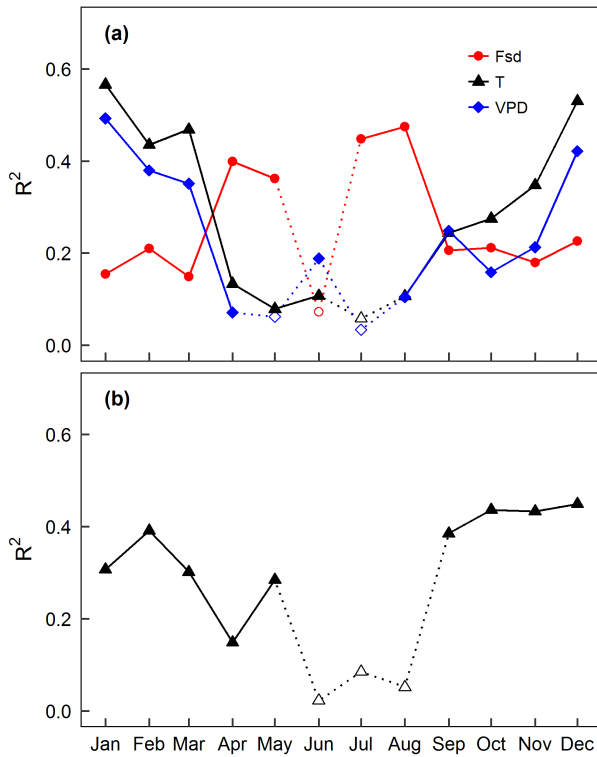


Figure 6. Seasonal variability in environmental controls of daytime and night-time NEE. Coefficients of determination (R^2) of (a) the rectangular hyperbolic light-response curve (LRC) between daily means of midday NEE and incoming radiation (F_{sd} ; red lines and circles), linear fits between residuals of LRC and air temperature (T_a ; black lines and triangles) or vapour pressure deficit (VPD; blue lines and diamonds) and (b) the temperature-response function after Lloyd and Taylor (1994) between daily means of u^* -filtered night-time NEE and air temperature (T_a ; black lines and triangles) per month pooled over 3 years. Open symbols indicate non-significant R^2 values; data points per month for panel (a) from January to December: 62, 74, 77, 76, 58, 42, 56, 60, 74, 75, 66, 72; data points per month for panel (b) from January to December: 55, 69, 63, 66, 52, 45, 41, 57, 63, 63, 52; 68.

in 2010 and 49 % in 2011. On seasonal timescales, the dependence of night-time NEE on T_a strongly varied, being greatest during spring (39–44 %, mean = 42 %) followed by summer (31–45 %, mean = 38 %) and lowest during autumn (15–30 %, mean = 24 %) (Fig. 6b). No significant relationships could be determined during winter months in which greater data gaps occurred compared to other months. Neither LT fitted for SWC bins (Table 5) nor linear relationships between SWC and LT residuals showed an influence of SWC on night-time NEE or its temperature sensitivity, with the exception of the winter month July when night-time NEE decreased with increasing SWC ($R^2 = 0.26^{***}$).

Table 4. Parameters, standard errors and/or the coefficient of determination (R^2) of the rectangular hyperbolic light-response curve (LRC) between daily means of midday NEE and incoming radiation (F_{sd}) for various T_a bins, VPD bins and SWC bins. α : initial slope of LRC and canopy light-utilization efficiency ($\mu\text{mol CO}_2 \text{ J}^{-1}$); β : maximum NEE (i.e. uptake rate of the canopy) at light saturation ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Significance level: *** < 0.001; ns: not significant. nr: number of data points.

| LRC | α (SE) | β (SE) | R^2 | nr |
|------------------------------|-----------------|-----------------|-------|-----|
| T_a bins | | | | |
| < 8 | −0.14 (0.02)*** | −23.6 (0.0)*** | 0.39 | 133 |
| 8–12 | −0.09 (0.01)*** | −29.3 (0.0)*** | 0.55 | 205 |
| 12–16 | −0.07 (0.01)*** | −30.4 (0.0)*** | 0.50 | 172 |
| 16–20 | −0.07 (0.01)*** | −27.9 (0.0)*** | 0.37 | 124 |
| 20–24 | −0.08 (0.02)*** | −20.7 (0.0)*** | 0.19 | 97 |
| 24–28 | −0.06 (0.03) ns | −20.5 (0.1)*** | 0.13 | 49 |
| VPD bins | | | | |
| < 0.4 | −0.10 (0.01)*** | −28.7 (0.0)*** | 0.46 | 324 |
| 0.4–0.8 | −0.07 (0.01)*** | −30.5 (0.0)*** | 0.44 | 232 |
| 0.8–1.2 | −0.05 (0.01)*** | −32.9 (0.0)*** | 0.47 | 103 |
| 1.2–1.6 | −0.62 (1.39) ns | −16.7 (0.7)*** | 0.00 | 68 |
| 1.6–2.0 | −0.16 (0.25) ns | −16.3 (0.5)*** | 0.02 | 25 |
| 2.0–2.4 | −0.06 (0.05) ns | −18.7 (0.2)*** | 0.09 | 26 |
| 2.4–2.8 | −0.05 (0.03) ns | −15.1 (0.2)*** | 0.47 | 7 |
| 2.8–3.2 | – | – | – | – |
| > 3.2 | −0.08 (0.27) ns | −12.7 (0.8)*** | 0.05 | 4 |
| SWC bins | | | | |
| < 0.22 | −0.11 (0.02)*** | −22.35 (0.0)*** | 0.18 | 258 |
| ≥ 0.22 | −0.14 (0.01)*** | −21.88 (0.0)*** | 0.29 | 534 |

Table 5. Parameters, standard errors and/or the coefficient of determination (R^2) of the temperature-response function after Lloyd and Taylor (1994) between daily means of u^* -filtered night-time NEE and air temperature (T_a) for subsets of data. R_{ref} : basal respiration rate at 10 °C ($\mu\text{mol CO}_2 \text{ J}^{-1}$); E : activation energy parameter. Significance level: *** < 0.001, ** < 0.01, * < 0.5; ns: not significant. nr: number of data points.

| LT | R_{ref} (SE) | E (SE) | R^2 | nr |
|-----------------|----------------|-------------|-------|-----|
| All data | 3.0 (0.1)*** | 310 (16)*** | 0.36 | 694 |
| 2010 | 3.6 (0.2)*** | 215 (23)*** | 0.31 | 214 |
| 2011 | 2.8 (0.2)*** | 405 (27)*** | 0.49 | 234 |
| 2012 | 2.8 (0.2)*** | 306 (31)*** | 0.30 | 246 |
| SWC bins | | | | |
| 0.1–< 0.15 | 2.1 (0.5)*** | 349 (94)*** | 0.34 | 37 |
| 0.15–< 0.20 | 3.0 (0.3)*** | 285 (44)*** | 0.27 | 138 |
| 0.20–< 0.25 | 3.1 (0.2)*** | 339 (34)*** | 0.38 | 146 |
| 0.25–< 0.30 | 3.4 (0.2)*** | 337 (30)*** | 0.38 | 200 |
| > 0.30 | 3.3 (0.2)*** | 527 (40)*** | 0.42 | 173 |

3.4 Annual estimates of NEE, GPP, and ER and associated uncertainties

From the various partitioning methods applied, the DINGO output with the night-time data approach using NN and u^* -filtered early evening hours resulted in ER estimates most consistent with the soil respiration data; in terms of the relative contribution of soil respiration, exceeding 1 was minimal (see Supplement Fig. S2a). However, the daytime approach partitioning method using the LRC with the DINGO routine (3a) (Fig. S3a) yielded similar results, followed by the night-time approach using the Lloyd and Taylor temperature-response function (1) in which night-time fluxes only were filtered after the u^* threshold (Fig. S1c). Overall, the coefficient of variation in annual estimates of ER derived from different partitioning methods ranged from 8 to 10 %, while variation in annual estimates of NEE and GPP was small (4–7 and 2–4 %) (see Supplement Fig. S4, Table S2).

The forest was a considerable and continuous carbon sink during the 3-year study period, with a mean NEE of $-1234 \pm 109 \text{ g C m}^{-2} \text{ yr}^{-1}$. Estimates of annual NEE increased from $-1046 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2010 to $-1424 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2012 (Table 2). Estimates for annual ER were similar for 2010 and 2011, whereas in 2012 annual ER decreased (Table 2). Annual GPP estimates were slightly higher in 2010 compared to other years and were similar for 2011 and 2012 (Table 2). ER was on average 55 % of GPP, but this ranged between 61 % (2010) and 49 % (2012) (Table 2).

4 Discussion

4.1 Seasonal variability in CO₂ ecosystem fluxes

Gross and net CO₂ ecosystem fluxes showed strong seasonality in this dry temperate eucalypt forest. On a seasonal timescale, GPP exceeded ER almost continually, even in winter; thus, NEE showed a net carbon uptake across all seasons. Daily minimum and maximum rates of ER and daily minimum rates of GPP were within the reported range for temperate evergreen coniferous and deciduous broadleaved forests compiled by Falge et al. (2002). Although daily maximum GPP rates at our forest site ($14.7 \text{ g C m}^{-2} \text{ d}^{-1}$) were comparable with those from temperate evergreen coniferous forests ($16.6\text{--}26.3 \text{ g C m}^{-2} \text{ d}^{-1}$), they were much lower than those reported for temperate deciduous broadleaved forests ($22.4\text{--}31.0 \text{ g C m}^{-2} \text{ d}^{-1}$) during growing seasons (Falge et al., 2002).

Both GPP and ER peaked during summer and were lowest in winter, which is similarly typical for temperate evergreen coniferous forests (Baldocchi, 2008; Baldocchi and Valentini, 2004). However, during spring the increase in ER lagged behind that of GPP, an occurrence similarly typical for temperate deciduous broadleaved forests (Baldocchi, 2008;

Baldocchi and Valentini, 2004). Thus, NEE peaked in early spring and again in summer. A likely explanation for the delayed increase in ER as compared to GPP in springtime could be a limitation of microbial decomposition due to lower temperatures or substrate supply. Partitioning of soil respiration into its component fluxes of heterotrophic (microbial) and belowground autotrophic (plant) respiration in an earlier study (Hinko-Najera et al., 2015) showed that heterotrophic respiration was low during springtime but increased and peaked during (late) summer months corresponding to when total soil respiration fluxes were greatest (Fig. S2a). Similar seasonal variability in GPP and ER was observed in a wet temperate eucalypt forest; however, NEE peaked only during spring in this forest as GPP was limited by water availability during the dry summer period (Kilinc et al., 2013). These phenomena highlight that carbon exchange dynamics in this dry temperate eucalypt forest are different in their seasonal behaviour from temperate deciduous broadleaved or evergreen coniferous forests in the Northern Hemisphere (Baldocchi, 2008; Baldocchi and Valentini, 2004; Falge et al., 2002); thus, the latter should not be used as analogues.

4.2 Environmental drivers of CO₂ ecosystem fluxes

As indicated above, the overall main environmental drivers of NEE were radiation and temperature. Temporal variability in daytime NEE was equally strongly influenced by radiation, temperature and/or VPD, which did not vary throughout the 3-year study period. Interestingly, a strong seasonal variability in environmental controls on NEE was revealed. While radiation was the dominant environmental driver of daytime NEE in mid to late autumn and winter, temperature was the main environmental control from spring to early autumn. In accordance with daytime NEE, temperature sensitivity of night-time NEE followed a distinct seasonal pattern, with greater influence of T_a on night-time NEE during spring and summer months. An indication of a limitation of respiration due to high water content in July is, however, precarious as data availability was lowest (< 50 %) during this month.

Dry temperate eucalypt forests, like most of Australia's forests, are generally characterized by dry summer periods and are thus greatly influenced by changes in water availability (Haverd et al., 2013a). However, environmental drivers related to water availability such as VPD and SWC had either a small or no influence on daytime NEE fluxes during summer months and night-time NEE fluxes. Thus, there was no apparent water limitation on carbon dynamics during our study period in this forest. This is in contrast with findings from Keith et al. (2012), van Gorsel et al. (2013) and Kilinc et al. (2013) for wet temperate eucalypt forests. In all these studies ecosystem carbon fluxes were limited by VPD and/or SWC during dry summer months, with the greatest effects on daytime NEE rather than night-time NEE. However, this can be explained by the anomalously high rainfall at our forest site due to strong La Niña events from mid-2010 to early

2011 and early 2012 (BoM, 2012) during most of the study period. The lack of SWC influence on carbon fluxes until the end of 2012 was also evident in concurrent studies on soil respiration dynamics at the same study site in which SWC did not decline below a certain threshold to limit soil respiration (Hinko-Najera et al., 2015).

4.3 Annual carbon balance and uncertainties

The dry temperate eucalypt forest was a very strong and continuous carbon sink for all 3 years. Our mean annual ER / GPP ratio (~ 0.55) was lower than the mean ER / GPP ratio of 0.76 for Australian ecosystems (Beringer et al., 2016), the 0.80 reported for temperate forests (Janssens et al., 2001; Luysaert et al., 2007) and the 0.77 derived from a global database (Baldocchi, 2008). Moreover, our annual estimates for NEE are greater than published estimates for forest ecosystems around the globe collated by Baldocchi et al. (2001) or Luysaert et al. (2007), and our annual estimates are at the upper end of the probability distribution for sites within the global FLUXNET network (Baldocchi, 2014).

That temperate eucalypt forests in Australia exhibit large carbon uptake has been shown in wet temperate eucalypt forests (> 1000 mm annual rainfall) only recently. A tall old-growth *E. regnans* forest had an NEE of $-930 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Beringer et al., 2016). A wet temperate *E. delegatensis* forest near Tumberumba (Keith et al., 2009, 2012; van Gorsel et al., 2013) was a strong sink of $\sim 900 \text{ g C m}^{-2} \text{ yr}^{-1}$ during years with average annual rainfall (~ 1400 mm), but this sink was reduced ($\sim 750 \text{ g C m}^{-2} \text{ yr}^{-1}$) during the above-average rainfall ($\sim 2000\text{--}2200$ mm) years of 2010 and 2011 (van Gorsel et al., 2013). Overcast conditions and thus reduced incoming solar radiation explained this reduced sink (van Gorsel et al., 2013). However, NEE estimates we report for our study site are higher than those reported from the Tumberumba eucalypt forest during the same years of above-average rainfall. A possible explanation for the greater net carbon uptake estimates in our dry temperate eucalypt forest might be the higher leaf area index (~ 1.8) (Griebel et al., 2016; Moore, 2011) than in the wet temperate eucalypt forest (~ 1.4) near Tumberumba, conferring a higher canopy photosynthetic capacity. Our study supports the conclusion of Keith et al. (2009) that temperate eucalypt forests have a high carbon uptake potential because they are evergreen, and as such photosynthetic carbon uptake can occur throughout the year when conditions are favourable. Indeed, a detailed study of stem and canopy growth dynamics at our study site demonstrated that the trees in fact grow all year, with canopy expansion observed mainly in summer and early autumn, and the stem growth mainly in spring and autumn, but also to a lesser degree in winter (Griebel et al., 2017). Another possible explanation for the higher net carbon uptake estimates at our study site is the absence of summer dry periods and a stimulation of growth due to the high rainfall. Prior to the period of high rainfall in 2010–2012, forests throughout tem-

perate Australia experienced a decade-long drought that negatively affected NEE and net primary production (Haverd et al., 2013b). Keith et al. (2012) and Kilinc et al. (2013) also reported that drought conditions in the wet temperate eucalypt forest strongly reduced NEE by having a greater negative effect on GPP than ER. Therefore, it is likely that the onset of high rainfall in winter and early spring 2010 led to favourable conditions for growth and high carbon uptake given the opportunistic behaviour of eucalypts to changing environmental conditions (Jacobs, 1955; Keith, 1997).

However, the possibility of a remaining underestimation of ER cannot be excluded, although it can be accounted for during data processing and partitioning and by the addition of a storage term. We observed low night-time fluxes of NEE, and hence ER, which indicated a decoupling within the forest canopy and thus advection fluxes during night. Hence, it is possible that the high NEE values reported here are partly due to an underestimation of ER due to advection. However, such an error is likely to be a systematic one, meaning that an overestimation of NEE would have consistently occurred during the different measurement years and seasons. Results from a recent study to validate more recent annual NEE estimates with a biomass inventory (biomass increment and carbon content) indicated that the NEE estimates from the EC measurements were systematically 30 % greater than the net primary production of the tree biomass from inventory methods (Bennett, 2016, unpublished data). It is a reasonable assumption that tree net primary production contributed the majority to NEE and as such the inventory data would be a confirmation that the flux tower underestimates ER, resulting in a greater NEE. However, the underestimation was indeed of a similar magnitude in each of the measurement years and confirmed the high carbon uptake rate of this dry temperate eucalypt forest when compared to other ecosystems.

Our data indicate that the main environmental controls for daytime NEE (radiation and temperature) and night-time NEE (temperature) did not vary between years. We observed moderate variations in NEE amongst the 3 years, with an increase in NEE from 2010 through to 2012. The high rainfall in late 2010 and early 2011 most likely led to favourable forest growth conditions throughout 2011 and a stronger increase in GPP rather than ER and thus an increase in NEE from 2010 to 2011, most evident in autumn and winter. This 2011 increase in NEE is in accordance with the observed 2011 global sink anomaly (Haverd et al., 2013a, 2016; Poulter et al., 2014), which has been mainly attributed to semi-arid ecosystems in Australia (Eamus and Cleverly, 2015; Haverd et al., 2013a). Hence, our results indicate that the global sink anomaly was not limited to only semi-arid ecosystems. The further increase in NEE from 2011 to 2012 was indicated by a reduction in ER as GPP remained steady. Rainfall was lower in 2012 as compared to the previous 2 years and thus soil water content decreased towards the end of 2012 (summer), likely influencing ER but not GPP. Given that ER is often dominated by soil respiration, this pattern is

in agreement with findings on soil respiration patterns from concurrent studies in the same forest (Hinko-Najera et al., 2015) in which low soil water contents led to a decrease in soil respiration.

5 Conclusion

Temperate eucalypt forests are underrepresented in global assessments concerning terrestrial and/or forest carbon dynamics and productivity (Baldocchi, 2008; Falge et al., 2002; Luysaert et al., 2007), and so far no data have been available on ecosystem carbon exchange dynamics from dry temperate eucalypt forests. This study shows that not only wet temperate eucalypt forests but also dry temperate eucalypt forests have a large carbon uptake potential, particularly during above-average rainfall, and thus adds further evidence that temperate eucalypt forests are strong carbon sinks during favourable conditions (Keith et al., 2009). Furthermore, carbon dynamics in this dry temperate eucalypt forest, similar to other temperate eucalypt forests, do differ in their seasonal behaviour compared to temperate evergreen coniferous and deciduous broadleaved counterpart forests in the Northern Hemisphere. The evergreen nature of the trees, coupled with mild winter temperatures, allow for the year-round physiological activity of eucalypts, which can lead to continuous growth throughout the year. When this is coupled with high rainfall in the warmer summer months, it can lead to very large carbon uptake. However, long-term measurements over multiple years are required to further evaluate the net carbon sink strength of dry temperate eucalypt forests, particularly in years with drought conditions, a scenario predicted to increase in occurrence and intensify in southeastern Australia (Christensen et al., 2013; CSIRO, 2012). Furthermore, studies using alternative approaches, for example independent upscaled ER estimates from component flux measurements (Keith et al., 2009; Lavigne et al., 1997; Law et al., 1999; Phillips et al., 2010; Speckman et al., 2015), are needed to account for underestimation in ER due to advection fluxes and to validate measurements from the EC flux tower.

Data availability. The OzFlux QA–QC data set presented in this paper is available from the OzFlux Data Portal (Arndt, 2013) and the DINGO data set presented in this paper is available on figshare (Beringer and Hinko-Najera, 2017).

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Competing interests. The authors declare that they have no conflict of interest.

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