

Using data assimilation to understand the effect of disturbance on the carbon dynamics of a managed woodland

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Key Points:

- Data assimilation used with the DALEC model to investigate effect of selective felling
- New observation operator constructed to allow assimilation of finer temporal resolution information
- No change found in NEE post-disturbance due to concurrent reduction in respiration and GPP

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Abstract

The response of forests and terrestrial ecosystems to disturbance is an important process in the global carbon cycle in the context of a changing climate. In order to better understand ecosystem response to selective felling in a managed forest site we use the mathematical technique of data assimilation to combine a diverse set of observations with a mathematical model of ecosystem carbon balance. We develop new data assimilation techniques allowing for the assimilation of daytime and nighttime net ecosystem exchange observations with a daily time-step model. This allows for the assimilation of additional carbon flux information which would otherwise be neglected. The techniques allow us to estimate the effect of step-changes in ecosystem composition on the parameter and state variables in a modelled estimate of forest carbon balance. These techniques are applicable to other ecosystem models and data assimilation schemes. Previous statistical analyses of eddy covariance data at the study site had suggested that disturbance from selective felling (thinning) resulted in no significant change to the net carbon uptake of the ecosystem. Our results support this with a predicted net ecosystem carbon uptake for the year 2015 of $426 \pm 116 \text{ g C m}^{-2}$ for the unthinned forest and $420 \pm 78 \text{ g C m}^{-2}$ for the thinned forest despite a reduction in gross primary productivity of 337 g C m^{-2} . We show that this is likely due to reduced ecosystem respiration post-disturbance compensating for a reduction in gross primary productivity. This supports the theory of an upper limit of forest net carbon uptake due to the magnitude of ecosystem respiration scaling with gross primary productivity.

1 Introduction

The response of forests and terrestrial ecosystems to disturbance (e.g. felling, fire, or insect outbreaks) is one of the least understood components in the global carbon cycle [Ciais *et al.*, 2014]. Current land surface models fail to represent the effect of disturbances on long-term carbon dynamics [Running, 2008], although these disturbances could have a significant effect on net land surface carbon uptake. Indeed, there could be significant variations in the effect as the range of forest disturbance can be wide: from stand replacing disturbance (where tree mortality is close to 100%) to non-stand replacing disturbance, (where only a proportion of total trees are lost). This paper uses data assimilation to improve the modelling of the non-stand replacing disturbance of selective felling (thinning) on forest carbon dynamics.

Thinning is a silvicultural practice used to improve ecosystem services or the quality of a final tree crop and is globally widespread. The effect of thinning on carbon budgets has largely been ignored [Liu *et al.*, 2011]. It would be logical to assume that after thinning we would see a reduction in the net carbon uptake of an ecosystem, presumably due to reduced Gross Primary Productivity (GPP) following a reduction in total leaf area and unchanged or heightened ecosystem respiration due to an input of brash and woody debris to the forest floor. However, previous studies, analysing flux-tower eddy covariance records, find no significant change in the observed net ecosystem exchange (NEE) of CO₂ after thinning [Vesala *et al.*, 2005; Wilkinson *et al.*, 2015; Moreaux *et al.*, 2011; Dore *et al.*, 2012]. These studies suggest this is due to increased light availability and reduced competition allowing ground vegetation to display increased GPP and compensate for an increase in heterotrophic respiration post-disturbance.

Other studies have shown a significant reduction in the carbon content of rhizosphere soils following tree felling [Hernesmaa *et al.*, 2005]. It has been shown that tree roots provide a rhizosphere priming effect, greatly increasing the rate of soil organic carbon decomposition [Dijkstra and Cheng, 2007], suggesting a decrease in respiration following thinning. This is consistent with previous work carried out at the study site in this paper, where it has been shown that the magnitude of ecosystem respiration is strongly coupled to the magnitude of GPP [Heinemeyer *et al.*, 2012]. Predictions made by Kurz *et al.* [2008] about the impacts of mountain pine beetle outbreaks in Northern American forests suggested a switch from sink to source of carbon following this disturbance. However, the analysis of a diverse set of observations for an area with approximately 70% infested trees by Moore *et al.* [2013] revealed little change in net CO₂ flux, due to concurrent reductions in gross primary productivity and ecosystem respiration. Similar results are also found from large scale tree girdling experiments [Högberg *et al.*, 2001], where 1-2 months after girdling a 54% decrease in soil respiration is observed.

Data assimilation is a mathematical technique for combining observations with prior model predictions in order to find the best estimate to a studied system. Functional ecology models have been combined with many different observations relevant to the carbon balance of forests [Zobitz *et al.*, 2011; Fox *et al.*, 2009; Richardson *et al.*, 2010; Quaipe *et al.*, 2008; Zobitz *et al.*, 2014; Niu *et al.*, 2014], leading to improved estimates of model parameter and state variables and reduced uncertainty in model predictions. Although there have been many efforts to model the effect of disturbance on forest ecosystems [Seidl

et al., 2011; Thornton et al., 2002], the use of data assimilation has been limited, with only a few examples, all of which used satellite data [Kantzas et al., 2015; Hilker et al., 2009]. The authors are not aware of any studies assimilating site level data to quantify disturbance effects. By assimilating observations relevant to post-disturbance ecosystem carbon dynamics with prior model predictions of ecosystem behaviour, we can analyse the retrieved parameters after data assimilation to find the model predicted effects of disturbance.

In this paper we investigate the effect of thinning on the carbon dynamics of the Alice Holt flux site [Wilkinson et al., 2012], a deciduous managed woodland, following an event in 2014, when one side of the site was thinned and the other side left unmanaged. We present new methods for the assimilation of daytime and nighttime NEE observations with a daily time-step model, in this case the Data Assimilation Linked Ecosystem Carbon (DALEC2) model [Bloom and Williams, 2015]. These methods require no model modification. We combine all available observations for 2015 with prior model predictions to find two sets of optimised model parameter and initial state values, corresponding to thinned and unthinned sides of the forest. We then use these two versions of the model to seek an explanation for why the net uptake of carbon remains unchanged even after removing a large proportion of the trees from one side. We find a net ecosystem carbon uptake for the year 2015 of $426 \pm 116 \text{ g C m}^{-2}$ for the unthinned forest and $420 \pm 78 \text{ g C m}^{-2}$ for the thinned forest, despite a reduction in GPP of 337 g C m^{-2} for the thinned forest when compared to the unthinned forest. We find that reduced ecosystem respiration for the thinned forest allows for this unchanged net carbon uptake. The data assimilation techniques presented in this paper could be applied for similar analyses at other sites and provide a novel method to help elucidate the reasons behind ecosystem responses.

2 Observation and data assimilation methods

2.1 Alice Holt research forest

Alice Holt Forest is a research forest area managed by the UK Forestry Commission located in Hampshire, SE England. Forest Research has been continuously operating a CO₂ flux measurement tower in a portion of the forest, the Straits Inclosure, since 1998. The Straits Inclosure is a 90 ha area of deciduous broadleaved plantation woodland on a surface water gley soil, which has been managed for the past 80 years. The majority of

the canopy trees are oak (*Quercus robur* L.), with an understory of hazel (*Corylus avellana* L.) and hawthorn (*Crataegus monogyna* Jacq.), but there is a small area of conifers (*Pinus nigra* J. F. Arnold) within the tower measurement footprint area depending on wind direction. Further details of the Straits Inclosure site and the measurement procedures are given in *Wilkinson et al.* [2012], together with analysis of stand-scale 30 minute average net CO₂ fluxes (NEE) measured by standard eddy covariance methods from 1998-2011.

As part of the management regime, the Straits Inclosure is subject to thinning, whereby a proportion of trees are removed from the canopy in order to reduce competition and improve the quality of the final tree crop. At the Straits an intermediate thinning method is used with a portion of both subdominant and dominant trees being removed from the stand [*Kerr and Haufe*, 2011]. The whole of the stand was thinned in 1995. Subsequently the Eastern side of the Straits was thinned in 2007 and then the Western side in 2014. The flux tower at the site is situated on the boundary between these two sides, allowing for the use of a footprint model to split the flux record and analyse the effect of this disturbance on carbon fluxes at the site. In *Wilkinson et al.* [2015] a statistical analysis of the eddy covariance flux record found that there was no significant effect on the net carbon uptake of the Eastern side after thinning in 2007. In this paper we focus on the effect of disturbance on the Western side after thinning in 2014. We therefore refer to the Western side as “thinned” forest and the Eastern side as “unthinned” forest.

2.2 Observations

In order to assess the effect the 2014 thinning had on the Straits Inclosure, an intensive field campaign was undertaken in 2015 to measure leaf area index and also estimate woody biomass. From the site we also have a long record of flux data as discussed in section 2.1. These observations span both the thinned and unthinned sides of the forest.

2.2.1 Leaf area index

To assess the impact of the 2014 thinning, three transects were established in the Straits Inclosure for intensive sampling during 2015. A total of 435 sampling points were marked at 10 m apart, using a GPS and fluorescent tree spray paint. Measurements of peak LAI (July 2015 - September 2015) were made using both a ceptometer and hemispherical photography. The transects were walked twice with the ceptometer taking read-

ings at every sampling point, giving 870 readings in total. Hemispherical photographs were taken every 50 m as shown in Figure 1, giving 89 photographs in total.

We measure below canopy Photosynthetically Active Radiation (PAR) using the ceptometer while logging above canopy PAR using a data logger and PAR sensor positioned outside the canopy. We can then estimate LAI using the above and below canopy PAR readings [Fassnacht *et al.*, 1994]. For the hemispherical photographs, we use the HemiView software [Rich *et al.*, 1999] which can calculate the proportion of visible sky as a function of sky direction (gap fraction) this can then be used to calculate LAI [Jonckheere *et al.*, 2004].

Six litter traps were also established at points along the transects allowing for comparison with the other methods. These were sampled throughout the season in 2015. We found the LAI derived from the litter traps was always greater than LAI estimates derived from optical methods, as expected [Bréda, 2003]. From the sampling of the litter traps we also have estimates of leaf mass per area for use in data assimilation. As the 6 litter traps are not enough to describe the LAI for the research site [Kimmins, 1973], we used estimates from the ceptometer and hemispherical photographs for data assimilation. We take the weighted average of the hemispherical photograph and ceptometer estimated LAI to find an LAI of 4.42 with a standard error of 0.07 for the Eastern unthinned section of forest, and an LAI of 3.06 with a standard error of 0.07 for the Western thinned section of forest. We are assimilating the mean of 299 LAI observations in the unthinned and 225 in the thinned section of forest. Consequently the appropriate representation of error for data assimilation is the standard error of the mean. From our litter trap observations we find a leaf mass per area of 29 g C m^{-2} for both sides of the forest.

2.2.2 Woody biomass

The method of Point-Centred Quarters (PCQ) was used to conduct a biomass survey as specified in Dahdouh-Guebas and Koedam [2006]. Along the three transects 114 points were sampled measuring the Diameter at Breast Height (DBH) and the density of trees. We then used allometric relationships between DBH and total above ground biomass and coarse root biomass, found in work carried out by Forest Research and in McKay *et al.* [2003], to find an estimate of total woody and coarse root carbon (referred to as C_{woo} in the DALEC2 model). These observations are shown in table 1.

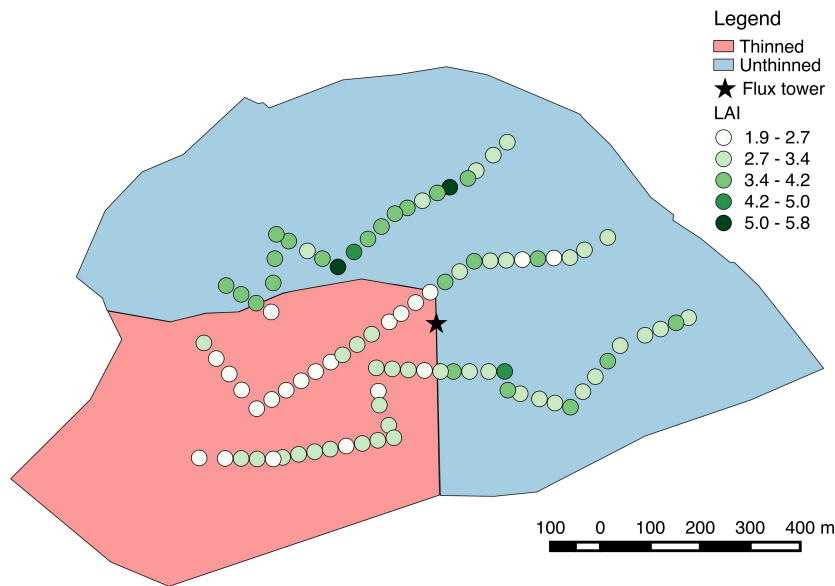


Figure 1. Hemispherical photograph derived LAI for the Straits Inclosure at 50m intervals along three transects.

Forest Research also carry out their own mensuration studies at the site. One such study was carried out on the Western side after the thinning at a similar time to our own PCQ measurements and found a tree density of 225 ha^{-1} and an average DBH of 32 cm, which are in close agreement to our own estimates in table 1. This gives us confidence that other measurements taken from Forest Research from before the thinning will be representative of the methods we have used. From 2009, measurements from Forest Research found the Western side to have a tree density of 418 ha^{-1} and an average DBH of 27.73 cm. This suggests that approximately 46% of trees have been removed during thinning. From these estimates we can also see the effect thinning has on the type of trees found at the site. The amount of trees per hectare has dropped dramatically after thinning but the mean DBH has increased, because the smaller subdominant trees have been removed. The mean DBH on the Eastern side is greater still, indicating that the thinning that took place in 2007 of the Eastern side has allowed the dominant trees to grow as a result of reduced competition.

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Table 1. Point-centred quarter method observations for 2015.

Sector	Tree density (ha ⁻¹)	Mean DBH (cm)	Estimated woody biomass and coarse root carbon (g C m ⁻²)
Unthinned (E)	272	34.12	13130
Thinned (W)	225	32.85	9908

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2.2.3 Flux tower eddy covariance

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The Straits Inclosure flux tower provides us with half-hourly observations from January 1999 to December 2015, these consist of the NEE fluxes and meteorological driving data of temperature, irradiance and atmospheric CO₂ concentration for use in the DALEC2 model. The NEE data was subject to u^* filtering (with a value of 0.2 m s⁻¹) and quality control procedures as described by *Papale et al.* [2006], but was not gap-filled. The resultant half-hourly NEE dataset is then split between observations corresponding to the Western thinned and Eastern unthinned sides of the site using a flux-footprint model, see *Wilkinson et al.* [2015] for more details.

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To match the timestep of our model we compute daily NEE observations by taking the mean over the 48 measurements made each day, selecting only days where there is no missing data. As we have been strict on the quality control of the flux record and not allowed any gap filling, this presents a problem in terms of the number of daily NEE observations available to us. By further splitting the flux record between two sides we retrieve very few total daily observations of NEE for either side. In order to address this we instead compute day and nighttime NEE fluxes (NEE_{day} and NEE_{night} respectively) for use in data assimilation. To compute daytime or nighttime NEE observations, we take the mean over the half-hourly day or nighttime (calculated using a solar model) measurements, again only taking periods where there are no gaps in the data so that we are only considering true observations. This provides us with many more observations for assimilation, as seen in table 2. Because we are averaging over shorter time periods we have a smaller probability of gaps and erroneous data. We see that we have many more daytime NEE observations than nighttime, as we tend to have much more turbulent air mixing in

daylight hours. In section 2.3.2 we give details of how we relate these twice daily observations of NEE to a daily time-step model.

Table 2. Number of observations of NEE, NEE_{day} and NEE_{night} for East and West sides of the Straits Inclosure for the year 2015.

Sector	NEE	NEE_{day}	NEE_{night}
Unthinned (E)	22	60	42
Thinned (W)	26	54	48

The error in observation of daily NEE are assumed to be constant and set at $0.5 \text{ g C m}^{-2}\text{day}^{-1}$ by *Williams et al.* [2005], whereas *Braswell et al.* [2005] find these errors to be closer to $1 \text{ g C m}^{-2}\text{day}^{-1}$. However, *Richardson et al.* [2008] show that flux errors are heteroscedastic. To account for the heteroscedastic nature of NEE errors we define an error function that scales between 0.5 to $1 \text{ g C m}^{-2}\text{day}^{-1}$ based on the magnitude of the observation. This function is defined as $0.5 + 0.04|NEE_{day}^i| \text{ g C m}^{-2}\text{day}^{-1}$, where $|NEE_{day}^i|$ is the magnitude of the daytime NEE observation. *Raupach et al.* [2005] comment that nighttime measurements of NEE are much more uncertain than daytime measurements. This is difficult to quantify, but here we assume that nighttime flux errors are 3 times the magnitude of daytime errors. We therefore have the error function of $1.5 + 0.12|NEE_{night}^i| \text{ g C m}^{-2}\text{day}^{-1}$, where $|NEE_{night}^i|$ is the magnitude of the nighttime NEE observation. We also include correlations in time between the errors in our observations of NEE, as discussed in *Pinnington et al.* [2016].

2.3 Model and data assimilation

2.3.1 DALEC2 ecosystem carbon model

The DALEC2 model is a simple process-based model describing the carbon dynamics of a forest ecosystem [*Bloom and Williams, 2015*]. The model is constructed of six carbon pools (labile (C_{lab}), foliage (C_{fol}), fine roots (C_{roo}), woody stems and coarse roots (C_{woo}), fresh leaf and fine root litter (C_{lit}) and soil organic matter and coarse woody debris (C_{som})) linked via fluxes. The aggregated canopy model (ACM) [*Williams et al., 1997*] is used to calculate daily gross primary production (GPP) of the forest, taking me-

eteorological driving data and the modelled leaf area index (a function of C_{fol}) as arguments. Figure 2 shows a schematic of how the carbon pools are linked in DALEC2, full model equations can be found in the appendix, section A.1.

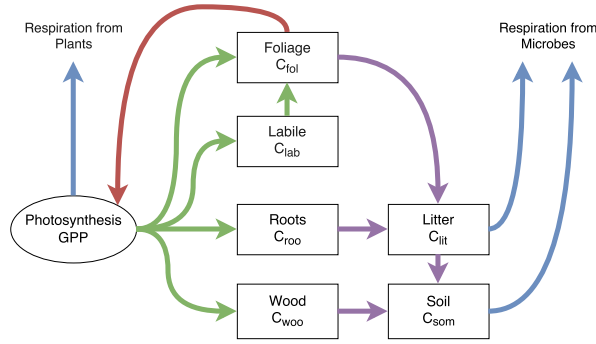


Figure 2. Representation of the fluxes in the DALEC2 carbon balance model. Green arrows represent C allocation, purple arrows represent litter fall and decomposition fluxes, blue arrows represent respiration fluxes and the red arrow represents the influence of leaf area index in the GPP function.

2.3.2 Data assimilation

We implement Four-Dimensional Variational data assimilation (4D-Var) with the DALEC2 model for joint parameter and state estimation. In 4D-Var we aim to find the parameter and initial state values such that the model trajectory best fits the data over some time window, given some prior information about the system. This prior information takes the form of an initial estimate of the parameter and state variables of the model, \mathbf{x}^b , valid at the initial time. This prior is assumed to have unbiased, Gaussian errors with known covariance matrix \mathbf{B} . Adding the prior term ensures that our problem is well posed and that we can find a locally unique solution [Tremolet, 2006]. The prior used in this paper is derived from the assimilation of eddy covariance data from previous years and can be found in table A.1. In 4D-Var we aim to find the parameter and initial state values that minimises the weighted least squares distance to the prior, while minimising the weighted least squares distance of the model trajectory to the observations over a time window of length N , with individual time points t_0, \dots, t_N [Lawless, 2013]. We do this by finding the state \mathbf{x}^a at time t_0 that minimises the cost function

$$J(\mathbf{x}_0) = \frac{1}{2}(\mathbf{x}_0 - \mathbf{x}^b)^T \mathbf{B}^{-1}(\mathbf{x}_0 - \mathbf{x}^b) + \frac{1}{2} \sum_{i=0}^N (\mathbf{y}_i - \mathbf{h}_i(\mathbf{x}_i))^T \mathbf{R}_i^{-1}(\mathbf{y}_i - \mathbf{h}_i(\mathbf{x}_i)), \quad (1)$$

where \mathbf{x}_0 is the vector of parameter and initial state values to be optimised, \mathbf{x}_i is the vector of variables at time t_i , \mathbf{h}_i is the observation operator mapping the parameters and state to the observations, \mathbf{y}_i is the vector of observations at time t_i and \mathbf{R}_i is the observation error covariance matrix. The size of the time step, i , is 1 day in this case. Further details of the implemented data assimilation scheme and specification of prior and observational errors can be found in *Pinnington et al.* [2016].

In this paper we assimilate day and nighttime NEE in order to increase the number of observations available to us and also better partition our modelled estimate of GPP and total ecosystem respiration. As the DALEC2 model runs at a daily time step, this requires us to relate the daily parameter and state values from the model to the twice-daily observations of NEE. We do this by writing two new observation operators, one relating the model state and parameters to daytime NEE, and the other to nighttime NEE. The NEE of CO_2 at any given time is the difference between GPP and ecosystem respiration. For an observation of total daily NEE on day i we have,

$$NEE^i = -GPP^i(C_{fol}^i, \Psi) + f_{auto}GPP^i(C_{fol}^i, \Psi) + \theta_{lit}C_{lit}^i e^{\Theta T^i} + \theta_{som}C_{som}^i e^{\Theta T^i}, \quad (2)$$

where all terms have the same meaning as described in the appendix section A.1, with the first being gross primary productivity, the second term corresponding to autotrophic respiration and the third and fourth terms corresponding to heterotrophic respiration. For total daytime NEE we have,

$$NEE_{day}^i = -GPP^i(C_{fol}^i, \Psi) + \delta_{day}f_{auto}GPP^i(C_{fol}^i, \Psi) + \delta_{day}\theta_{lit}C_{lit}^i e^{\Theta T_{day}^i} + \delta_{day}\theta_{som}C_{som}^i e^{\Theta T_{day}^i} \quad (3)$$

where δ_{day} is the day length, expressed as $\frac{\text{number of daylight hours}}{24}$, and T_{day}^i is the mean daytime temperature. Here we still have the same term for GPP as in equation (2) as all photosynthesis occurs during daylight hours. We have made the assumption that respiration is spread uniformly in time, therefore the respiration terms are scaled by the length of daylight hours. For nighttime NEE we have,

$$NEE_{night}^i = \delta_{night}f_{auto}GPP^i(C_{fol}^i, \Psi) + \delta_{night}\theta_{lit}C_{lit}^i e^{\Theta T_{night}^i} + \delta_{night}\theta_{som}C_{som}^i e^{\Theta T_{night}^i} \quad (4)$$

where δ_{night} is the night length, expressed as $\frac{\text{number of night hours}}{24}$, and T_{night}^i is the mean nighttime temperature. Here we no longer have a term for GPP as no GPP will occur

during the night. The respiration is again scaled by night length as in equation (3). Day length and night length are calculated using a solar model here, but could also be estimated using the record of incident solar radiation from the flux tower. These new observation operators allow for assimilation of day/nighttime NEE without the need for altering the model and can be applied to other ecosystem models to allow for the assimilation of finer temporal resolution eddy covariance data. From section 3 we can see that these modified observation operators allow our model to predict both daytime and nighttime NEE accurately.

2.4 Experimental setup

We run three data assimilation experiments for the one year window of 2015, in these experiments we assimilate different combinations of observations as shown in table 3. By performing this type of “data denial” procedure we can assess the relative levels of information from the different data streams and their impact on the disturbance effect predicted by the model. In each experiment we use the prior model as specified in table A.1. This prior model was found by assimilating daytime and nighttime NEE, leaf mass per area and LAI observations from 2012 and 2013 before the thinning occurred, more information on the methods used to find this prior model can be found in *Pinnington et al.* [2016].

In each experiment we run the assimilation for both the unthinned forest and the thinned forest. Combining the two distinct sets of observations for either side with our prior model using 4D-Var data assimilation. This allows us to retrieve two unique sets of parameter and initial state values, corresponding to the thinned and unthinned sections of the site. We are then able to judge the effect the thinning in 2014 had on the carbon dynamics of the forest in 2015. We do this by analysing the optimised parameter and initial state values for the thinned and unthinned forest and also considering the model predictions of different variables for each side post-disturbance.

We expect that we will retrieve different estimates for each of the experiments outlined in table 3, with our most confident estimate being when all observations types are assimilated together in experiment C. This allows us to see how much information each data stream provides us with and assess whether NEE data alone is enough to understand the effect of disturbance.

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Table 3. Combination of observations used in data assimilation experiments.

Experiment	NEE	LAI & leaf mass per area	C_{woo}
A	×		
B	×	×	
C	×	×	×

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3 Results

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In Figure 3 and 4 we show the observations and model trajectories after assimilation for the thinned and unthinned forest for experiments A and C respectively. We can see that the model fits all the assimilated observations well after assimilation for both experiments. We have confidence in our results as we have demonstrated previously that assimilating a single year of data can accurately hindcast the carbon uptake of the site for a long time period (15 years) into the future [Pinnington *et al.*, 2016]. From Figure 3a and 3b the modified observation operators presented in section 2.3.2 have allowed our model to represent both daytime and nighttime NEE well.

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In experiment A we have only assimilated NEE observations, from table 4 we can see that we improve the fit to the assimilated observations for both the unthinned and thinned forest when compared to the prior model. The root-mean-square error (RMSE) is within the specified observation error for both daytime and nighttime NEE after assimilation. By only assimilating observations of NEE we have not been able to accurately predict LAI or C_{woo} . For LAI although we have improved the models fit after assimilation for the thinned forest (see table 4) we have significantly degraded the model fit to LAI for the unthinned forest. This is because partitioning the NEE dataset between the thinned and unthinned forest (as described in section 2.2.3) has introduced a bias into our observation sampling. We can see from Figure 3a that for the period of greatest carbon uptake (June 2015 - August 2015) we have no observations for the unthinned forest (due to the prevailing wind in this period being from the SouthWest), this allows our model to under-predict the carbon uptake for the unthinned forest and thus also significantly under-predict LAI as seen in Figure 3c. From Figure 3d and table 4 we can see that NEE observations alone do not give us any information to recover a value of C_{woo} for the DALEC2 model.

In experiment B we assimilated NEE, LAI and leaf mass per area observations. From table 4 we see that including these extra observations have allowed the model to fit LAI well for both the unthinned and thinned forest, and although the model fit to the NEE observations is slightly degraded it is still well within the specified observation error from section 2.2.3. We also see that including these extra observations still does not allow us to recover an accurate value of C_{woo} .

In experiment C we assimilate all available observations. This gives us very similar results as in experiment B, except including the observations of C_{woo} in the assimilation allows the model to fit this observation well as seen in table 4. We see from Figure 4a and 4c that including observations of LAI in the assimilation removes the bias introduced from the partitioning of the NEE observations between the unthinned and thinned forest. The distinct difference in stand structure is now clear in Figure 4, with reduced LAI and woody carbon for the thinned forest. For experiment C the model predicted time of green-up and senescence in LAI is consistent with phenocam observations made by Forest Research at the site, included in supplementary material (Figure S12).

Table 5 shows the cumulative annual fluxes for the year 2015 for the three experiments. In all three experiments there is no significant difference between the net carbon uptake for the thinned and unthinned forest. We can see that both experiments B and C predict very similar cumulative fluxes, suggesting that the assimilated observations of C_{woo} have not had much impact on the model carbon dynamics for this time period. We believe observations of C_{woo} will become much more important over longer time-scales. Here we have only assimilated a single observation of C_{woo} for either side of the forest, if multiple observations of C_{woo} were available throughout time this would give us an estimate to woody biomass increment, providing an important constraint on the carbon assimilation of the forest. Experiments A and C both predict no significant difference in the net ecosystem carbon uptake between the thinned and unthinned forest. However, the partitioning of this carbon uptake between GPP and total ecosystem respiration (RT) is significantly different, with experiment A predicting increased RT and GPP after thinning and experiment C predicting reduced RT and GPP after thinning, this can be seen more clearly in Figure 5. This highlights the issue that NEE is the difference between two large fluxes ($NEE = -GPP + RT$) and we can therefore find an accurate prediction of NEE despite under/overestimating both GPP and RT. This means we have to be careful when interpreting model results based solely on NEE data, especially in this case as we have seen that the

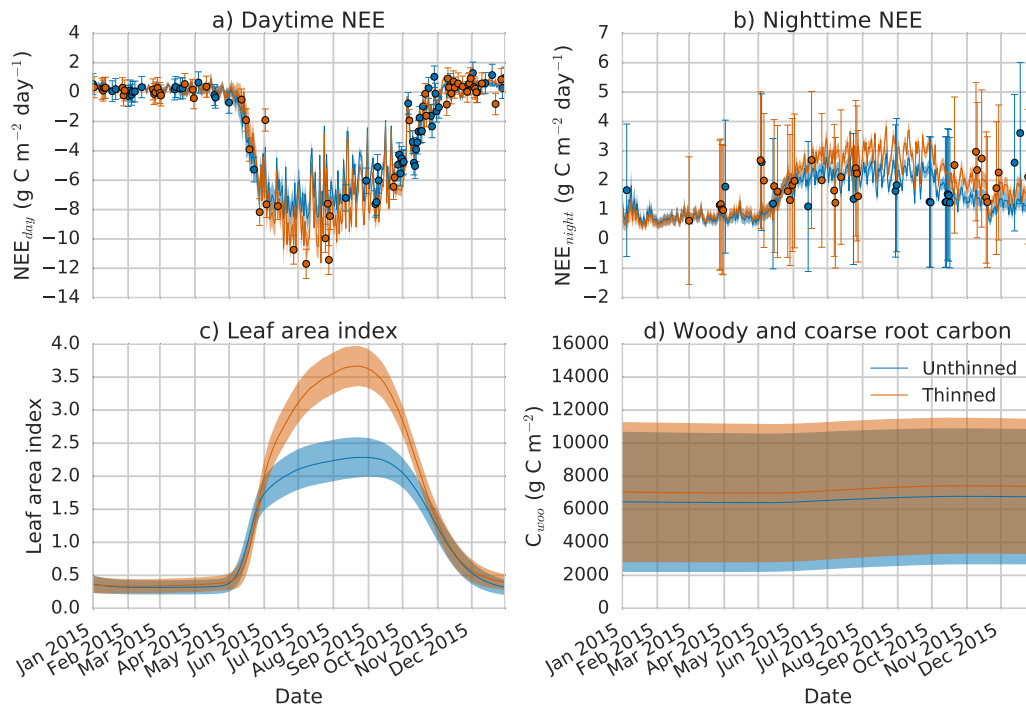


Figure 3. Experiment A: 2015 unthinned and thinned forest observations and model trajectories after assimilation. Blue line: model trajectory after assimilation of unthinned data, blue shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), blue dots: unthinned observations with error bars, orange line: model trajectory after assimilation of thinned data, orange shading: uncertainty in model trajectory after assimilation (± 1 standard deviation), orange dots: thinned observations with error bars.

partitioning of this NEE data between the thinned and unthinned forest has introduced a bias into our dataset. If we were to base our analysis on experiment A we would assume that the thinning had caused an increase in ecosystem respiration and that this had been compensated for by an increase in GPP. This is the opposite conclusion to the one we find in experiment C when we include observations relating to the structure of the forest.

In Figure 6 we show the partitioning of cumulative ecosystem respiration for the year 2015 between total autotrophic respiration and heterotrophic respiration from litter and soil for both the unthinned and thinned forest in experiment C. Here we can see the strong dependence of autotrophic respiration on GPP with the growth rate being much greater between June 2015 - September 2015 (when GPP will be of greater magnitude), for heterotrophic respiration the growth rate is more constant throughout the whole year. Total ecosystem respiration is reduced by 331 g C m⁻² for the thinned forest when com-

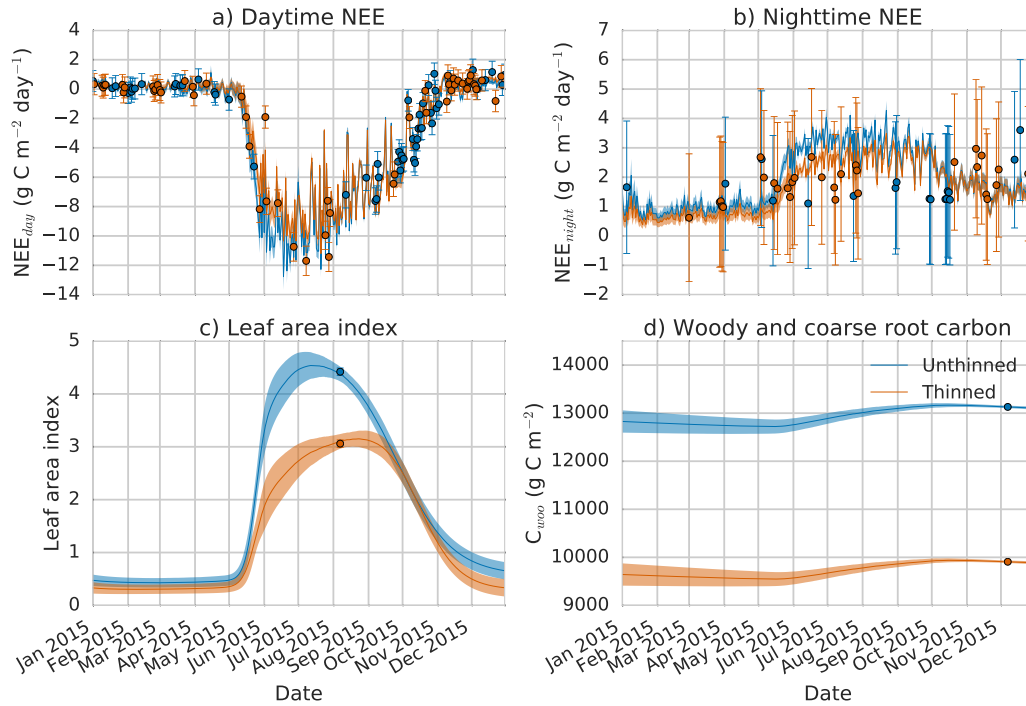


Figure 4. Experiment C: 2015 unthinned and thinned forest observations and model trajectories after assimilation. Colour, lines and dots have the same meaning as described in Figure 3.

pared to the unthinned forest, with reductions in both heterotrophic and autotrophic respiration of 169 g C m⁻² and 162 g C m⁻² respectively.

Figure 7 shows the change in parameter and initial state values for the thinned and unthinned forest after assimilating all observations in experiment C. It is important to note this is the difference when compared to our prior model estimate, which was found by assimilating only eddy covariance, LAI and leaf mass per area observations from 2012 and 2013. We therefore expect changes in parameter and state values for both the thinned and unthinned forest, as we are assimilating new data streams. This is particularly noticeable in the carbon pool state members in Figure 7. Constraints on the carbon pool state members are provided by the assimilated observations of woody biomass and coarse roots (C_{woo}), LAI and leaf mass per area (c_{lma}). LAI and c_{lma} give us a constraint on foliar carbon (C_{fol}) as $LAI = \frac{C_{fol}}{c_{lma}}$. We can see the values for the model predicted carbon pools are as we might expect with the thinned forest having less carbon in all pools when compared to the unthinned forest. For litter carbon (C_{lit}) we expect a reduction in input of leaf litter for the thinned forest, and although there might be increased woody debris after

Table 4. Root-mean-square error of model fit to observations for the prior model and all experiments after data assimilation.

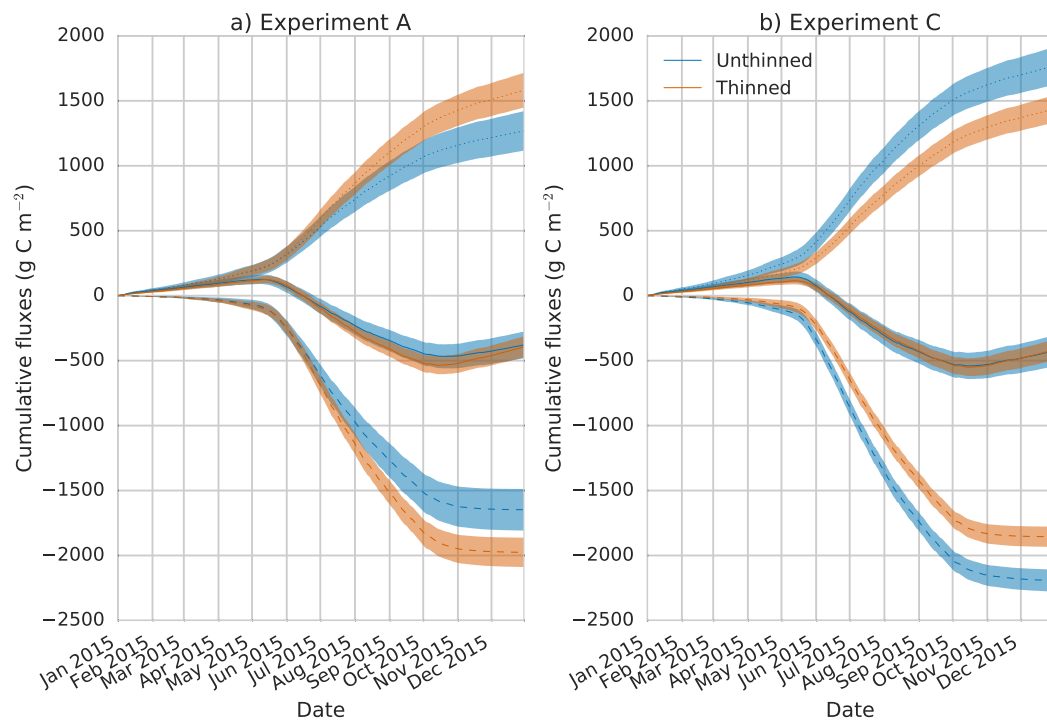
Unthinned forest				
Exp.	NEE _{day}	NEE _{night}	LAI	C _{woo}
Prior	1.25 g C m ⁻² day ⁻¹	1.02 g C m ⁻² day ⁻¹	0.43	5507 g C m ⁻²
A	0.61 g C m ⁻² day ⁻¹	0.83 g C m ⁻² day ⁻¹	2.16	6361 g C m ⁻²
B	0.75 g C m ⁻² day ⁻¹	0.93 g C m ⁻² day ⁻¹	0.04	5987 g C m ⁻²
C	0.75 g C m ⁻² day ⁻¹	0.93 g C m ⁻² day ⁻¹	0.04	0.16 g C m ⁻²
Thinned forest				
Exp.	NEE _{day}	NEE _{night}	LAI	C _{woo}
Prior	1.05 g C m ⁻² day ⁻¹	0.61 g C m ⁻² day ⁻¹	1.79	2285 g C m ⁻²
A	0.63 g C m ⁻² day ⁻¹	0.54 g C m ⁻² day ⁻¹	0.55	2505 g C m ⁻²
B	0.63 g C m ⁻² day ⁻¹	0.56 g C m ⁻² day ⁻¹	0.04	2241 g C m ⁻²
C	0.63 g C m ⁻² day ⁻¹	0.56 g C m ⁻² day ⁻¹	0.04	0.07 g C m ⁻²

thinning this is much less readily decomposed and so possibly has little impact in the year after thinning. The difference in predicted soil carbon content (C_{som}) between the thinned and unthinned forest is consistent with studies analysing soil carbon contents after felling [Hernesmaa *et al.*, 2005]. For the parameters the biggest changes appear to be in the litter carbon turnover rate parameter (θ_{lit}), with the retrieved parameter being significantly reduced for the unthinned forest when compared to the thinned. However we still see reduced total litter respiration in Figure 6 for the thinned forest compared to the unthinned forest, this is due to the significant difference in litter carbon content (C_{lit}) for both sides, with the unthinned forest having a much high litter carbon content than the thinned forest. The large change in the θ_{lit} parameter between the two sides is therefore compensating for an overestimated difference in litter carbon content between the two sides.

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Table 5. Total annual fluxes and standard deviations for 2015 after assimilation (g C m^{-2}).

Unthinned forest			
Flux	Experiment A	Experiment B	Experiment C
NEE	-379 ± 99	-425 ± 113	-426 ± 116
GPP	1648 ± 159	2191 ± 87	2193 ± 83
RT	1267 ± 150	1766 ± 146	1767 ± 146
Thinned forest			
Flux	Experiment A	Experiment B	Experiment C
NEE	-394 ± 81	-421 ± 73	-420 ± 78
GPP	1976 ± 112	1855 ± 75	1856 ± 80
RT	1582 ± 134	1435 ± 100	1436 ± 109



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Figure 5. Experiment A & C: 2015 unthinned and thinned forest model trajectories for cumulative fluxes after assimilation. Solid line: cumulative NEE, dotted line: cumulative ecosystem respiration, dashed line: cumulative GPP. Colour and shading has the same meaning as in Figure 3.

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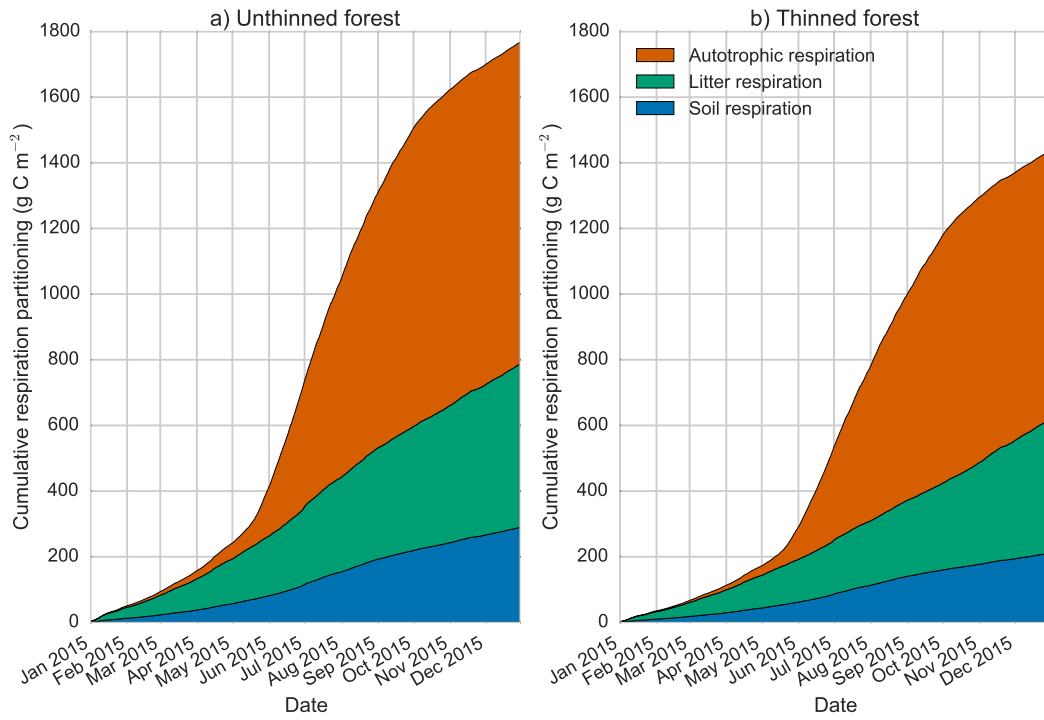


Figure 6. Experiment C: 2015 unthinned and thinned forest model trajectory for cumulative total ecosystem respiration after assimilation and its partitioning between total autotrophic respiration and heterotrophic respiration from litter and soil.

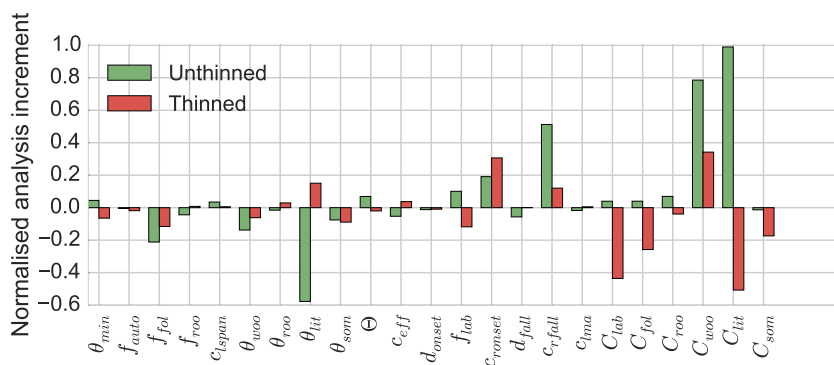


Figure 7. Experiment C: normalised analysis (posterior model) increment ($\frac{\mathbf{x}^a(i) - \mathbf{x}^b(i)}{\mathbf{x}^b(i)}$) for the unthinned and thinned forest. Explanation of parameter and state variable symbols in table A.1.

4 Discussion

In this paper we have used data assimilation to combine observations and prior model predictions of ecosystem carbon balance in order to understand how the state of an ecosystem might be altered after a disturbance event. We conducted three experiments assimilating different combinations of available data streams. For all experiments we find no significant change in net carbon uptake for the studied ecosystem following stand thinning, where approximately 46% of trees were removed. This is consistent with other studies of ecosystem carbon dynamics following thinning. We find different reasons for this unchanged carbon uptake dependent on which data streams are assimilated. When only assimilating NEE observations we find increased ecosystem respiration and increased GPP post-disturbance. These results are unreliable due to bias introduced into the NEE dataset from partitioning between the thinned and unthinned forest, this highlights the need for caution when interpreting model results based solely on NEE data. From our most confident estimate, where all available observations are assimilated, we find evidence that reductions in GPP following a decrease in total leaf area post-thinning are being offset by simultaneous reductions in ecosystem respiration. This is in contrast to current suggestions that reduced canopy photosynthesis is compensated for by increased GPP by ground vegetation post-thinning [Vesala *et al.*, 2005; Wilkinson *et al.*, 2015; Moreaux *et al.*, 2011; Dore *et al.*, 2012], however does support work investigating the effect of insect disturbance [Moore *et al.*, 2013].

Our results show a decrease in both autotrophic and heterotrophic respirations following thinning. Autotrophic respiration has both above and below ground components, whereas heterotrophic respiration is mainly from soils and litter. We follow the definition of Heinemeyer *et al.* [2012] and characterise below ground autotrophic respiration as respiration from roots, mycorrhizal fungi and other micro-organisms dependent on the priming of soils with labile carbon compounds from roots. It has been shown recently that deep root systems and their influences may be more widespread than previously thought [Pierret *et al.*, 2016]. Heterotrophic respiration is respiration by microbes not directly dependent on autotrophic substrate, however the largest fraction of heterotrophic respiration is based on the decomposition of young organic matter (e.g. leaves and fine roots) whose availability also depends on the GPP of an ecosystem [Janssens *et al.*, 2001]. We find similar decreases in both heterotrophic and autotrophic respiration for the thinned forest when compared with the unthinned forest. While it has been shown that heterotrophic respira-

tion can decrease after disturbance events [Bhupinderpal *et al.*, 2003], it is possible we overestimate the reduction in heterotrophic respiration and underestimate the reduction in autotrophic respiration. This is understandable as we have assimilated no data on this partitioning. Also our model description of autotrophic respiration is simple (described as a constant fraction of GPP) and therefore the heterotrophic respiration component of the model might compensate and in this instance describe the behaviour of mycorrhizal fungi and other microbes commonly categorised in the autotrophic component of respiration.

In a study measuring soil CO₂ fluxes over 4 years at the Straits Inclosure (the study site in this paper) Heinemeyer *et al.* [2012] showed a large 56% contribution of autotrophic respiration (characterised as root and mycorrhizal respiration) to total measured soil respiration. Heinemeyer *et al.* [2012] also suggested that mycorrhizal fungi play a role in priming the turnover of soil organic carbon by other microbes, with evidence from other studies [Talbot *et al.*, 2008]. Högberg and Read [2006] find similar figures for the autotrophic contribution to total soil respiration, with around half or more of all soil respiration being driven by recent photosynthesis. Heinemeyer *et al.* [2012] discuss the possibility of this tight coupling between GPP and ecosystem respiration leading to an upper limit for forest CO₂ uptake due to increased GPP leading to increased respiration, this is also discussed by Heath *et al.* [2005]. Our results support this theory, as we see ecosystem respiration scaling with GPP after approximately 46% of trees are removed from the study site, meaning that we find no significant change in net ecosystem carbon uptake after thinning.

Studies analysing eddy covariance flux records also find no significant change in the net ecosystem exchange of CO₂ after thinning [Vesala *et al.*, 2005; Wilkinson *et al.*, 2015; Moreaux *et al.*, 2011; Dore *et al.*, 2012]. These studies suggest that this is due to increased GPP by ground vegetation (following increased light availability and reduced competition) compensating for increases in heterotrophic respiration and reduced canopy photosynthesis post-thinning. We do not find evidence to support this and instead suggest that reduced ecosystem respiration is the most important component for the unchanged NEE of the forest following thinning. However, it is important to note that our observations of LAI are made at approximately 1 m above the forest floor. This means that our observations of LAI do not account for ground vegetation and therefore any effect of this ground vegetation is not simulated by our model. Despite this, observations made during multiple walks of the three established transects find no evidence of increased ground vegetation in the year after thinning. In fact much of the ground vegetation and subcanopy

was removed during thinning and did not appear to have recovered in the following year. At longer time-scales we believe re-growth of the subcanopy and ground vegetation will play an important role in increased productivity. Our results suggest that this increased productivity would also be met with subsequent increases in ecosystem respiration.

The effect of disturbance is poorly characterised in current land surface and global climate models [Running, 2008], it is therefore important to better understand how parameters and carbon pools might change following disturbance. DALEC2 and many other ecosystem models assume that respiration rates are proportional to carbon pool size. It has been suggested that although this assumption works well in equilibrium conditions it may not allow such models to predict ecosystem carbon dynamics following disturbance [Schimel and Weintraub, 2003]. The data assimilation techniques in this paper present a way for these simple models to cope with step changes in ecosystem behaviour, by allowing parameters and carbon pools to be updated following disturbance events.

5 Conclusion

In this work we have presented novel methods for understanding ecosystem responses to disturbance by using data assimilation. Assimilating all available data streams after an event of disturbance with a prior model prediction allows us to assess changes to model parameter and state variables due to this disturbance. We have also created modified observation operators to allow for the assimilation of daytime and nighttime NEE observations with a daily time-step model. This negates the need for model modification and increased the number of observations by a factor of 4.25.

We find no significant change in net ecosystem carbon uptake after a thinning event in 2014 where approximately 46% of trees were removed from the studied area. This was also found to be true when a similar event occurred in 2007 [Wilkinson *et al.*, 2015]. From our optimised model we find that reduced ecosystem respiration is the main reason for this unchanged net ecosystem carbon uptake. So that even for a decrease in GPP following thinning, there is no significant change in NEE. We believe this reduction in ecosystem respiration is due to reduced input of autotrophic substrate following thinning, meaning both autotrophic and heterotrophic respiration are reduced. These results support work suggesting that GPP is the dominant driver for ecosystem respiration [Janssens *et al.*, 2001; Heinemeyer *et al.*, 2012; Bhupinderpal *et al.*, 2003; Högberg and Read, 2006; Moore

et al., 2013]. This has implications on future predictions of land surface carbon uptake and whether forests will continue to sequester atmospheric CO₂ at similar rates, or if they will be limited by increased GPP leading to increased respiration.

A: Appendix

A.1 DALEC2 equations

The model equations for the carbon pools at day i are as follows:

$$GPP^i = ACM(C_{fol}^{i-1}, c_{lma}, c_{eff}, \Psi) \quad (A.1)$$

$$C_{lab}^i = C_{lab}^{i-1} + (1 - f_{auto})(1 - f_{fol})f_{lab}GPP^i - \Phi_{on}C_{lab}^{i-1}, \quad (A.2)$$

$$C_{fol}^i = C_{fol}^{i-1} + \Phi_{on}C_{lab}^{i-1} + (1 - f_{auto})f_{fol}GPP^i - \Phi_{off}C_{fol}^{i-1}, \quad (A.3)$$

$$C_{roo}^i = C_{roo}^{i-1} + (1 - f_{auto})(1 - f_{fol})(1 - f_{lab})f_{roo}GPP^i - \theta_{roo}C_{roo}^{i-1}, \quad (A.4)$$

$$C_{woo}^i = C_{woo}^{i-1} + (1 - f_{auto})(1 - f_{fol})(1 - f_{lab})(1 - f_{roo})GPP^i - \theta_{woo}C_{woo}^{i-1}, \quad (A.5)$$

$$C_{lit}^i = C_{lit}^{i-1} + \theta_{roo}C_{roo}^{i-1} + \Phi_{off}C_{fol}^{i-1} - (\theta_{lit} + \theta_{min})e^{\Theta T^{i-1}}C_{lit}^{i-1}, \quad (A.6)$$

$$C_{som}^i = C_{som}^{i-1} + \theta_{woo}C_{woo}^{i-1} + \theta_{min}e^{\Theta T^{i-1}}C_{lit}^{i-1} - \theta_{som}e^{\Theta T^{i-1}}C_{som}^{i-1}, \quad (A.7)$$

where T^{i-1} is the daily mean temperature, Ψ represents the meteorological driving data used in the GPP function and Φ_{on}/Φ_{off} are functions controlling leaf-on and leaf-off. Descriptions for each model parameter used in equations (A.1) to (A.7) are included in table A.1. DALEC2 can be parameterised for both deciduous and evergreen sites with Φ_{on} and Φ_{off} being able to reproduce the phenology of either type of site. The full details of this version of DALEC can be found in *Bloom and Williams* [2015].

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Table A.1. Parameter values and standard deviations for prior vector used in experiments.

Parameter	Description	Prior estimate (\mathbf{x}^b)	Standard deviation	Range
θ_{min}	Litter mineralisation rate (day^{-1})	5.471×10^{-4}	6.828×10^{-7}	$10^{-5} - 10^{-2}$
f_{auto}	Autotrophic respiration fraction	4.492×10^{-1}	1.814×10^{-4}	$0.3 - 0.7$
f_{fol}	Fraction of GPP allocated to foliage	4.091×10^{-2}	1.211×10^{-4}	$0.01 - 0.5$
f_{roo}	Fraction of GPP allocated to fine roots	3.700×10^{-1}	3.389×10^{-3}	$0.01 - 0.5$
c_{lspan}	Determines annual leaf loss fraction	1.089×10^0	2.777×10^{-3}	$1.0001 - 10$
θ_{woo}	Woody carbon turnover rate (day^{-1})	1.012×10^{-4}	3.040×10^{-9}	$2.5 \times 10^{-5} - 10^{-3}$
θ_{roo}	Fine root carbon turnover rate (day^{-1})	5.411×10^{-3}	1.353×10^{-6}	$10^{-4} - 10^{-2}$
θ_{lit}	Litter carbon turnover rate (day^{-1})	4.387×10^{-3}	1.825×10^{-6}	$10^{-4} - 10^{-2}$
θ_{som}	Soil and organic carbon turnover rate (day^{-1})	1.311×10^{-4}	2.705×10^{-9}	$10^{-7} - 10^{-3}$
Θ	Temperature dependance exponent factor	9.354×10^{-2}	6.810×10^{-5}	$0.018 - 0.08$
c_{eff}	Canopy efficiency parameter	5.618×10^1	6.676×10^0	$10 - 100$
d_{onset}	Leaf onset day (day)	1.584×10^2	1.370×10^1	$1 - 365$
f_{lab}	Fraction of GPP allocated to labile carbon pool	7.927×10^{-2}	1.491×10^{-4}	$0.01 - 0.5$
c_{ronset}	Labile carbon release period (days)	1.891×10^1	6.011×10^1	$10 - 100$
d_{fall}	Leaf fall day (day)	3.049×10^2	1.046×10^2	$1 - 365$
c_{rfall}	Leaf-fall period (days)	5.447×10^1	1.502×10^2	$10 - 100$
c_{lma}	Leaf mass per area (g C m^{-2})	2.929×10^1	7.099×10^2	$10 - 400$
C_{lab}	Labile carbon pool (g C m^{-2})	7.309×10^1	1.672×10^3	$10 - 1000$
C_{fol}	Foliar carbon pool (g C m^{-2})	1.313×10^1	6.707×10^2	$10 - 1000$
C_{roo}	Fine root carbon pool (g C m^{-2})	2.103×10^2	2.024×10^4	$10 - 1000$
C_{woo}	Above and below ground woody carbon pool (gCm^{-2})	7.182×10^3	2.019×10^7	$100 - 10^5$
C_{lit}	Litter carbon pool (g C m^{-2})	1.697×10^2	4.958×10^4	$10 - 1000$
C_{som}	Soil and organic carbon pool (g C m^{-2})	1.950×10^3	8.344×10^5	$100 - 2 \times 10^5$

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