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Estimating carbon carrying capacity in natural forest ecosystems across heterogeneous landscapes: addressing sources of error

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Abstract

Evaluating contributions of forest ecosystems to climate change mitigation requires well-calibrated carbon cycle models with quantified baseline carbon stocks. An appropriate baseline for carbon accounting of natural forests at landscape scales is carbon carrying capacity (CCC); defined as the mass of carbon stored in an ecosystem under prevailing environmental conditions and natural disturbance regimes but excluding anthropogenic disturbance. Carbon models require empirical measurements for input and calibration, such as net primary production (NPP) and total ecosystem carbon stock (equivalent to CCC at equilibrium). We sought to improve model calibration by addressing three sources of errors that cause uncertainty in carbon accounting across heterogeneous landscapes: (1) data-model representation, (2) data-object representation, (3) up-scaling. We derived spatially explicit empirical models based on environmental variables across landscape scales to estimate NPP (based on a synthesis of global site data of NPP and gross primary productivity, $n = 27$), and CCC (based on site data of carbon stocks in natural eucalypt forests of southeast Australia, $n = 284$). The models significantly improved predictions, each accounting for 51% of the variance. Our methods to reduce uncertainty in baseline carbon stocks, such as using appropriate calibration data from sites with minimal human disturbance, measurements of large trees and incorporating environmental variability across the landscape, have generic application to other regions and ecosystem types. These analyses resulted in forest CCC in southeast Australia (mean total biomass of 360 $t\,C\,ha^{-1}$, with cool moist temperate forests up to 1000 $t\,C\,ha^{-1}$) that are larger than estimates from other national and international (average biome 202 $t\,C\,ha^{-1}$) carbon accounting systems. Reducing uncertainty in estimates of carbon stocks in natural forests is important to allow accurate accounting for losses of carbon due to human activities and sequestration of carbon by forest growth.

Keywords: carbon accounting baseline, forest carbon stocks, net primary production, total ecosystem carbon, uncertainty analysis

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Introduction

Understanding carbon dynamics of natural ecosystems, particularly forests, is crucial as the international community considers the need to reduce emissions from deforestation and forest degradation (REDD) as part of a comprehensive approach to mitigation of climate change. Critical components of the carbon cycle include (1) the stock of total ecosystem carbon (TEC) (i.e. in living and dead biomass and soil), and (2) the flux of annual net ecosystem exchange. The stock is important because the larger the TEC stock, the greater the magnitude of greenhouse gas emissions from deforestation and forest degradation; a source of emissions additional to those from burning fossil fuels. The magnitude of a positive flux is important because it determines the capacity of the system to offset emissions, while the magnitude of a negative flux is important because it determines the longevity of the carbon stock.

Accounting of carbon stocks and fluxes requires an appropriate baseline for consistency and monitoring change. Carbon carrying capacity (CCC) is an appropriate baseline in naturally forested landscapes. It is defined as the mass of carbon stored in an ecosystem in a state of dynamic equilibrium under prevailing environmental conditions and natural disturbance regimes, but excluding anthropogenic disturbance (Gupta & Rao, 1994; Keith *et al.*, 2009). CCC provides a baseline against which current carbon stocks (CCS) can be compared, with the difference between CCC and CCS giving the carbon sequestration potential (CSP). These are landscape-scale (*cf* site-scale) metrics that provide an approach to quantifying forest degradation and

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sequestration in terms of carbon losses and gains due to human land-use activity (Gupta & Rao, 1994; Falloon *et al*., 1998; Zhang & Justice, 2001; Laclau, 2003).

Dynamic carbon models that simulate the terrestrial carbon cycle using the conceptual framework described in Fig. 1 (e.g. Barrett, 2002; Brack *et al*., 2006; Roxburgh *et al*., 2006) require empirical estimates of carbon stocks and fluxes, including CCC and CCS, for calibration and verification. These models need to be calibrated empirically because theoretical understanding of biophysical processes alone is insufficient to mechanistically link biological processes across spatial and temporal scales (Enquist *et al*., 2003). Parameter values are set using observational data so that the model outputs replicate landscape conditions either at equilibrium or in a transient state. Model parameters that need to be calibrated empirically include system state variables (e.g. carbon stores in living and dead biomass and soil carbon); time-dependent forcing variables (e.g. meteorological variables that alter rates of photosynthesis and respiration); and time-independent model parameters (e.g. rate constants and partitioning ratios that allocate photosynthates to plant components) (see discussion in Raupach *et al*., 2005). Model parameters can be spatially uniform or heterogeneous (see discussion of error type 6: spatial extrapolation of site data, and error type 7: spatial scales of site and GIS data).

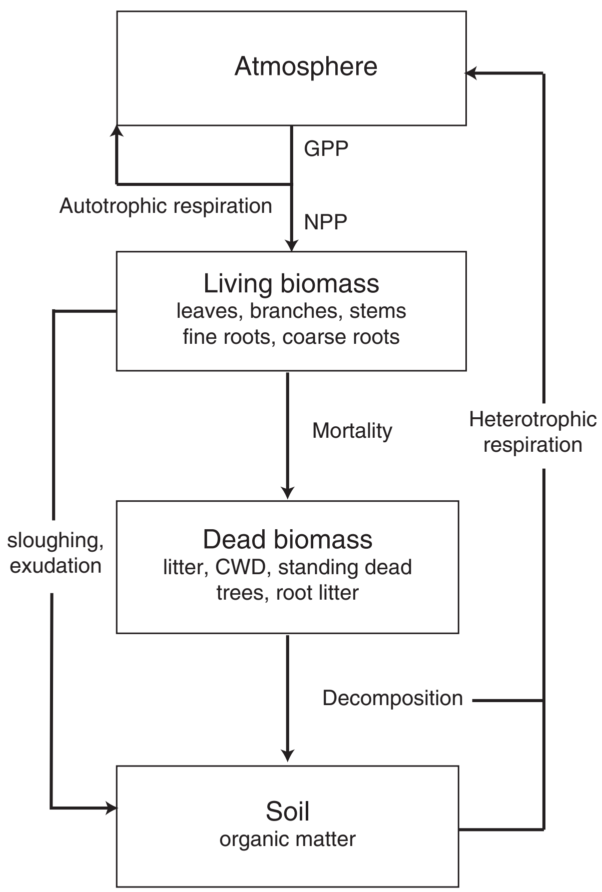

Fig. 1 Diagram of the ecological processes involved in estimating the carbon carrying capacity of natural forests. Boxes represent stocks of carbon and arrows represent fluxes of carbon.

Empirical data needed for model calibration are generally scarce and poorly representative across forest biomes. For example, globally there are only ~400 sites with measurements of net carbon exchange, although not all have complete budgets of pools and fluxes (Baldocchi *et al*., 2001; Falge *et al*., 2002), and just 27 forest sites have independent measurements of gross and net primary productivity (GPP and NPP; Table A3). Model–data fusion methods allow systematic use of all available data. Empirical data are used to calibrate model inputs of NPP and outputs of carbon pools contributing to TEC at equilibrium (in reality, usually a dynamic equilibrium where the maximum fluctuates within a range in response to external drivers). Then an inversion of the carbon cycle model can be used to estimate the internal flux parameters by function minimization and using any additional empirical data for model parameters to constrain the optimization procedure (Evans & Stark, 2002; Raupach *et al*., 2005; Roxburgh *et al*., 2006).

TEC is defined as the standing stock of carbon in all pools of a forested landscape, inclusive of the impact of (1) natural disturbance regimes (particularly fire) on carbon dynamics, and (2) environmental heterogeneity, when the ecosystem is at a dynamic equilibrium with climatic forcing variables. Hence, TEC as defined here is equivalent to CCC. Standing stock of biomass carbon depends on the rates of production, turnover, and decomposition. Spatial estimates of biomass are determined by tree growth rates as well as stand-level effects on total biomass production such as the rate of self-thinning and height growth due to competition. The input data of NPP represents the flux of carbon from the atmosphere to the ecosystem food web. NPP is the quantity of carbon available for biomass production after metabolic costs of autotrophic respiration (R_a) have been subtracted from GPP. NPP at a location (x) and over a specific time period (t) can be calculated in terms of carbon exchange or change in biomass (ΔB) plus turnover of biomass (T_B) (litterfall, coarse woody debris (CWD), root turnover and exudation, and herbivory) (Chapin *et al*., 2006):

$$\mathrm{NPP}_{(x,t)} = \mathrm{GPP}_{(x,t)} - R_{a(x,t)}, \tag{1}$$

$$\mathrm{NPP}_{(x,t)} = \Delta B_{(x,t)} + T_{B(x,t)}. \tag{2}$$

Model calibration, including estimation of NPP and TEC, is confounded at the landscape-level by natural heterogeneity due to (1) varying physical environmental conditions, (2) the impact of disturbance regimes (primarily fire but also pest outbreaks; Roland *et al*., 1999; Mackey *et al*., 2002), and (3) differences in plant species composition and associated life history characteristics. These factors interact to generate heterogeneous vegetation cover, rates of primary productivity and respiration, and thus spatially and temporally variable stocks and fluxes of carbon. Site data for calibration should sample the range of ecosystem conditions found in response to environmental conditions and natural disturbance regimes across a landscape.

Improvement in estimates of TEC stocks is important because these stocks are very large compared with annual fluxes. A change in stock, due to change in land use or management, results in large changes in the balance between terrestrial and atmospheric carbon stocks. The potential magnitude of uncertainty in estimates of carbon stocks and stock changes is high. For example, a 20% error in the input of NPP to carbon models, when derived from the ratio of NPP : GPP (i.e. a range of 0.4–0.6), could misrepresent the amount of carbon in the terrestrial biosphere by an amount equivalent to the total anthropogenic emissions of carbon dioxide (DeLucia *et al*., 2007).

In geographically extensive heterogenous landscapes, the uncertainty in calibration makes modelling carbon dynamics problematic. Raupach *et al*. (2005) argued that there is an urgent need for soundly based uncertainty characterizations for the main kinds of data used in terrestrial carbon observations. Similarly, the Intergovernmental Panel on Climate Change (IPCC) has recognized the need for improved forest-based mitigation analyses (IPCC, 2007; Nabuurs *et al*., 2007). Types of errors involved in terrestrial carbon calculations identified by Raupach *et al*. (2005) included measurement and representation errors. Based on experience with measurement and modelling of carbon pools and fluxes, we have redefined these types of errors as (1) data–model representation errors; (2) data–object representation errors; and (3) up-scaling errors. At least seven potential error types spanning these classes can be identified that confound estimation of NPP and TEC for the purposes of calibrating carbon models using model inversion (Table 1). Each of these error types are addressed in our analysis of CCC in natural forest ecosystems, and issues identified are itemized in 'Discussion.'

Data–model representation errors relate to assumptions about conversion of known variables to the parameters required in models. The first assumption relates to deriving NPP from differences in carbon fluxes. GPP can now be estimated using remote sensing and ancillary data (Berry & Roderick, 2004). However, the factors controlling respiration and their spatial variability are highly uncertain (Valentini *et al*., 2000). The components of NPP are difficult to measure in the field, and insufficient site data exist to parameterize complex models that describe processes of biomass production in relation to resource availability (Field *et al*., 1995). Hence, NPP is often approximated by assuming the ratio of NPP : GPP is a constant (Landsberg & Waring, 1997; Coops *et al*., 1998; Waring *et al*., 1998; Kirschbaum, 1999; Barrett, 2002; Raupach *et al*., 2002). However, there has been controversy over this issue with recent evidence suggesting nonlinear relationships influenced by environmental variables and natural disturbance regimes

Table 1 Potential sources of error in estimating carbon carrying capacity (CCC) and net primary productivity (NPP) that were investigated in this study and the class of error they represent (following Raupach *et al*., 2005)

Error type	Class of error
1. Interpretation of variable NPP Accuracy of the assumption that NPP : GPP is space/time invariant	Data-model representation error
2. Conversion of NPP to carbon stock is variable Accuracy of assumption that conversion of flux to stock (NPP : TEC) can be described as a constant allocation coefficient	Data-model representation error
3. Adequate sampling of forest type diversity Extent to which field data sample the diversity of forest ecosystems across the landscape	Data-object representation error
4. Site data below CCC Bias in available field data towards sites where carbon stocks are below their carbon carrying capacity	Data-object representation error
5. Accuracy of allometric equations Accuracy with which the available tree allometric equations estimate tree biomass beyond the site and species of derivation	Data-object representation error
6. Spatial extrapolation of site data Accuracy of environmental correlations used to spatially extrapolate biomass estimates from field sites to landscapes	Up-scaling error
7. Spatial scales of site and GIS data Bias in equating field site data with GIS data averaged over larger grid cells	Up-scaling error

(Keeling & Phillips, 2007). The second assumption is that the ratio of NPP : TEC (flux : stock) is a constant, described as an allocation coefficient in some models (Landsberg & Waring, 1997; Kirschbaum, 1999; Roxburgh *et al*., 2006), or as a logarithmic relationship. Both of these relationships assume optimal accumulation of biomass for a given NPP. However, for extensive heterogeneous landscapes it is important to include the effect of environmental conditions in determining the proportion of net production allocated to biomass increment compared with turnover.

Data–object representation errors occur because the data used to sample model objects may not be representative, and three error types need to be considered in the estimation of TEC. First, the extent to which the available data fail to sample adequately the diversity of forest types in a landscape. Forest ecosystems can vary considerably in their species composition, process rates, and carbon stocks. Some types are poorly sampled due to inaccessibility, lack of commercial value, or because they are not threatened or otherwise of priority for management. Second, bias in field data occurs due to sampling sites that are below CCC as the result of human land use but without knowing the extent of the reduction. The type, intensity and timing of land-use activities greatly influence carbon dynamics especially through the removal, destruction or accelerated decomposition of biomass and soil carbon. Loss of large old trees has a substantial impact on carbon stocks (Brown *et al*., 1997). In many parts of the world, naturally forested landscapes have a long history of land-use activities, and the current (i.e. extant) carbon stocks in these forest ecosystems may not represent CCC. Third, use of inappropriate allometric equations to estimate total tree biomass from site inventory data create a potential source of error. The mass of carbon stored in a single tree is estimated using allometric relationships between attributes readily measured in the field (tree diameter, height) and tree biomass that is measured only for a small number of trees. Conventional forest inventory mensuration is focused on estimating wood volume increments in regrowth stands, hence usually does not include samples of large old trees or nonmerchantable components (roots, bark, branches, stem butts, canopy). When these inventory trees are used to derive allometric equations, error can arise if nonlinear equations are extrapolated outside the tree size range from which they were derived in order to estimate biomass in mature forest ecosystems with large trees. Additionally, older trees can have internal decay that is not accounted for in estimating biomass from external stem volume measurements.

Up-scaling error is associated with the use of environmental correlates to extend spatially the site-based estimates of carbon stocks to cover the landscape of a region. As discussed by Raupach *et al*. (2005), a method for up-scaling is to introduce an empirical model that relates the fine-scale observations to coarse-scale state variables and additional fine-scale ancillary data such as topography and land surface attributes from remote sensing, and to combine these data sources in a geographic information system (GIS). Spatial extension of site-based carbon data is confounded by natural environmental heterogeneity as these data represent only samples along environmental gradients or a subset of the full compliment of environmental domains in a region (Mackey *et al*., 2008). A second source of up-scaling error arises because of the differences in scale of the sources of data being combined in the GIS. In particular, the areas of sites that provide observational data are often smaller than the pixel resolution of the climate, geology, soil, and remote sensing data. Hence, data at different spatial scales are being equated. There are also errors in the source spatial data used in the GIS modelling.

Our objectives in this study were to (1) improve methods for calibration of carbon models using field data, by testing approaches that address the potential sources of error identified in Table 1; and (2) use a case study of the extant natural eucalypt forests of south-eastern Australia to estimate NPP and CCC (which is equivalent to TEC at equilibrium) for a geographically extensive heterogeneous landscape. We calculate estimates of prediction ranges, as well as the mean, as an important component of the uncertainty analysis. Spatially quantifying NPP and CCC is the first step in calibrating a carbon model for estimating the region's CSP. Estimated carbon stocks for southeast Australia are compared with results from other national and international carbon accounting systems. We identify methods developed in our case study that have generic application to other ecosystem types.

Methods

Framework

Our approach for linking data at different scales was based on deriving empirical relationships between site data with spatially explicit environmental variables in order to spatially extend estimates of carbon stocks across landscapes. The framework linking data at tree, site, regional, and global scales is shown in Fig. 2 where the numbered steps are described in the following sections. The collation and calculation of site and spatial data are described in 'Methods' (steps 1–4) and the derivation of model parameters to predict NPP and CCC and their spatial extrapolation across the case study region are described in 'Results' (steps 5–8).

Table 2 Description of spatial data layers used for model development and extrapolation

Symbol	Layer description	Spatial resolution	Source
Climate – global			
P_{global}	Annual precipitation ($mm\,yr^{-1}$)		http://www.cru.uea.ac.uk/cru/data/tmc.htm and Table A3
T_{global}	Mean annual near surface air temperature (K)		http://www.cru.uea.ac.uk/cru/data/tmc.htm and Table A3
Q_a	Global top of atmosphere solar irradiance ($MJ\,m^{-2}\,yr^{-1}$)	10 min	Roderick (1999)
Q_{s_global}	Solar radiation received at the surface assuming 70% transmittance $$Q_{s\_global} = 0.7Q_a$$		Anderson (2005)
W	$$W = P - \frac{Qs}{\rho L}\ \mathrm{mm\,yr^{-1}}$$ where ρ is the density of liquid water (~1000 $kg\,m^{-3}$) and L is the latent heat of vaporization of water (~$2.45 \times 10^6\,J\,kg^{-1}\,H_2O$) W is a negative number	1 km	Berry & Roderick (2002)
W_{pos}	$W_{pos} = 1380 - W\,mm\,yr^{-1}$ W_{pos} allows calculation of the logarithm		
Climate – regional			
T	Mean annual near surface air temperature (°C)	1 km	ANUCLIM; Hutchinson (2005)
P	Annual precipitation ($mm\,yr^{-1}$)	1 km	ANUCLIM; Hutchinson (2005)
Q_s	Solar radiation received at the surface ($MJ\,m^{-2}\,yr^{-1}$)	1 km	ANUCLIM; Hutchinson (2005)
Vegetation – regional			
MVG	National Vegetation Information System. Australia – Present Major Vegetation Groups (MVG) – NVIS Stage 1, Version 3.0	100 m	National Vegetation Information System. Australia – Present Major Vegetation Groups – NVIS Stage 1, Version 3.0 (Albers 100 m analysis product). Australian Government Department of Environment, Water, Heritage and the Arts. http://www.environment.gov.au/erin/nvis/mvg/index.html
Veg	Classes: MVG 2 (Eucalypt Tall Open Forests; trees taller than 30 m); MVG 3 (Eucalypt Open Forests; trees 10–30 m tall)		
NDVI	MODIS 16-Day L3 Global 250 m (MOD13Q1) satellite imagery	250 m	Land Processes Distributed Active Archive Center and the National Aeronautic and Space Administration with final MODIS data products processed/re-formatted by CSIRO Marine and Atmospheric Research using the MODIS Reprojection Tool ('mrtmosaic,' 'resample')
GPP	Gross Primary Productivity (mol $CO_2\,m^{-2}\,yr^{-1}$)	250 m	See Appendix S4 and Berry *et al.* (2007)
Topographic – regional			
Elevation	Ground level elevation – Digital Elevation Model Version 3	9 s	Hutchinson *et al.* (2008)

Continued

Table 2. (*Contd.*)

Symbol	Layer description	Spatial resolution	Source
Topo	Topographic position index – calculated from the 250 m digital elevation model Classes: i – ridge top, ii – upper slope, iii – mid slope, iv – lower slope, v – valley	250 m	Gallant and Dowling (2003)
Edaphic – regional			
Geol	Classes: i – intrusive igneous, ii – extrusive igneous, iii – metamorphic, iv – sedimentary. Classes were derived from the surface lithology descriptions in the tables associated with the digitised map layers	1 : 1 000 000	Surface geology of Australia 1 : 1 000 000 scale (Liu *et al*., 2005a, b, c)
$\%OC$	Soil carbon concentration of A and B horizons (% C)	1 km	Australian Soil Resource Information System (ASRIS) McKenzie *et al*. (2005)
Sd_A, Sd_B	Soil depth of A and B horizons (m)	1 km	Australian Soil Resource Information System (ASRIS) McKenzie *et al*. (2005)
BD_A, BD_B	Soil bulk density of A and B horizons (mg m^{-3})	1 km	Australian Soil Resource Information System (ASRIS) McKenzie *et al*. (2005)
Sd_{AB}	$Sd_{AB} = Sd_A + Sd_B$ (m)	1 km	
SOC_A	$$SOC_A = Sd_A BD_A \frac{\%OC}{100}$$ (kg C m^{-2} of ground surface)	1 km	
SOC_B	$$SOC_B = Sd_B BD_B \frac{\%OC}{100}$$ (kg C m^{-2} of ground surface)	1 km	

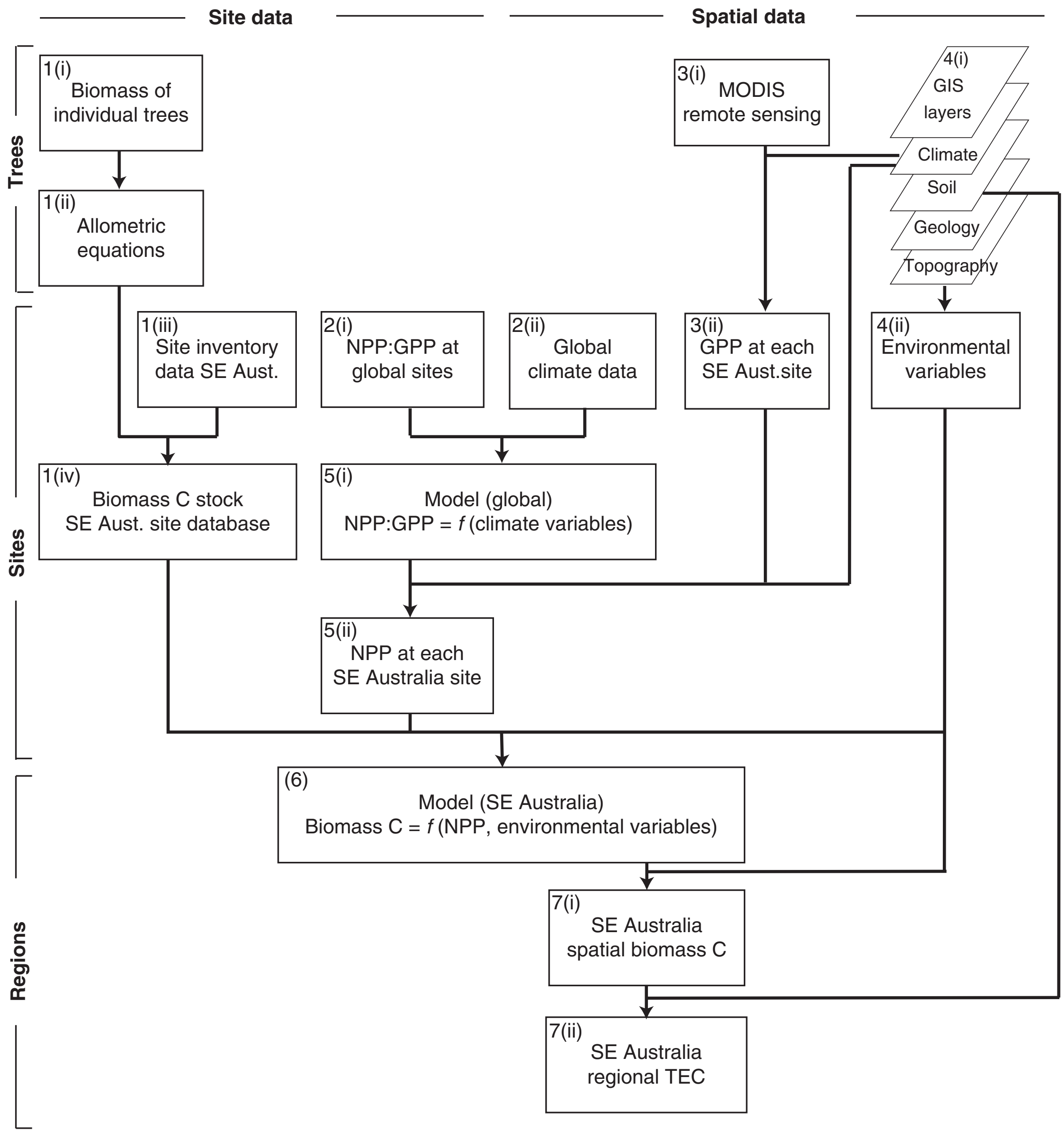

Fig. 2 Framework for linking data at different scales, which involves deriving empirical relationships between site data and spatially explicit environmental variables in order to spatially extend estimates of carbon stocks across landscapes. Numbered steps are described in 'Methods' and 'Results.'

Study area

The case study region was the extant natural eucalypt forests of southeast Australia, covering an area of around 14.5 million ha (Fig. 3). This area was defined by the spatial distribution of vegetation classes describing eucalypt forests where projective foliage cover of the upper stratum is between 30% and 70% and tree height >10 m (NVIS Major Vegetation Groups 2 and 3 in DEWHA, 2005). Areas of rainforest and riverine forests within the agricultural zone were excluded from the spatial analysis because they were not sampled by the available site data. Areas that were wetter than the range in water availability index (*W*, see Table 2) for the site data were excluded from the spatial analysis. Wet areas generally have high carbon stocks and so we were conservative in our estimates by not extrapolating beyond the numerical range sampled by the input data to the model.

Step 1: estimation of site biomass carbon stock

(i) *Tree biomass measurements*. Two methods were used to estimate biomass of individual trees (1) biomass measured from harvested trees where components were separated and

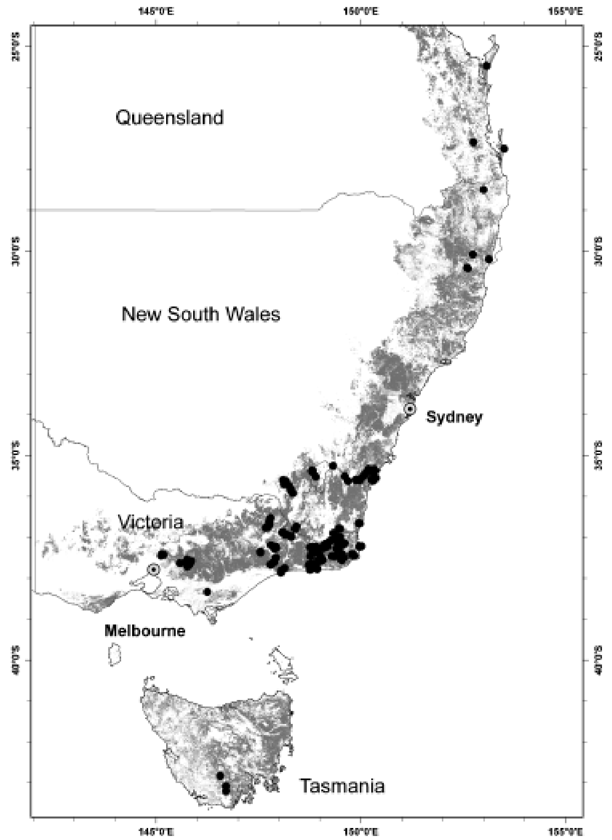

Fig. 3 Location of the case study site in southeast Australia showing the area of natural eucalypt forest and the field sites.

weighed; or (2) biomass estimated from stem volume (calculated from diameter, height and stem taper) plus sampled wood density, multiplied by an expansion factor to account for nonstem biomass components (leaves, twigs, branches, bark), and a reduction factor to account for internal wood decay. Measurement of tree component biomass includes decay and hollows in the stems. Estimation of biomass from stem volume assumes that wood density is uniform, hence does not include decay, which must be accounted for by applying a reduction factor to the calculated biomass. Very large eucalypts have buttresses at the base which means that a measurement of circumference at 1.3 m height may not represent biomass of the whole tree base. Details of these calculations for decay and buttresses are given in supporting information Appendix S1.

(ii) *Allometric equations*. Allometric equations are derived from biomass measured for a small number of individual trees and related to dimensions of the tree. This sample of trees must be representative of tree structure for the species and site. These relationships represent the architecture of the tree plus wood density, and hence vary considerably among species and site conditions. Equations appropriate for natural eucalypt forests in southeast Australia were compiled from the synthesis by Keith *et al*. (2000), as well as Dean & Roxburgh (2006), Dean (personal communication 2009), and Mackey *et al*. (2008). Where specific allometric equations were not available, the most appropriate equation was derived from averaged similar forest types, synthesized from the Australian literature (Keith *et al*., 2000). Details of these allometric equations are given in Appendix S1.

(iii) *Site inventory data*. Inventory data consist of measured dimensions of all trees within a plot area, usually diameter (at 1.3 m height) of trees $\geq$10 cm (in some plots trees $\geq$5 or $\geq$20 cm) and sometimes tree height. Inventory site data used for our case study were obtained from a range of published and unpublished studies with a total of 284 sites. Table A2 in Appendix S2 provides a summary on a regional basis of key site attributes and modelled variables used in this analysis. The key criterion for site selection was that the forest stands were largely undisturbed by intensive human land-use activity, and so represented samples of the landscape's CCC. Locations of the sites within the case study region, for which we obtained inventory data, are shown in Fig. 3.

(iv) *Site biomass carbon stock*. Carbon stock components include living biomass above- and belowground, dead biomass in litter above- and belowground, and CWD. Variable amounts of site data were available for each of these components. Many tree biomass measurements sampled only aboveground living material. Many inventory plots sampled only living trees, not the dead trees, litter, and CWD. There was no information about dead biomass in belowground litter. Biomass of living aboveground trees was calculated for all inventory plots using the most appropriate allometric equation for the species and site, and summing the biomass of all trees in the plot area. Biomass of dead standing trees was calculated from inventory tree diameter using an allometric equation for stem wood only. This biomass was reduced proportionally according to the decay reduction factor (Roxburgh *et al*., 2006) and where height measurements indicated that the top of a dead tree had fallen off. Where dead trees had not been measured in the inventory, an average value was used based on the synthesis by Woldendorp *et al*. (2002). Belowground biomass was calculated from allometric equations where root components had been measured. Where no equation existed, an average root : shoot ratio was applied based on the synthesis by Snowdon *et al*. (2002). Aboveground litter biomass is usually measured in quadrats, and CWD along transects in inventory plots. Where there were no measurements, average values were used from Woldendorp *et al*. (2002).

Step 2: global site database of NPP : GPP

A global dataset of forest sites ($n = 27$) was compiled where NPP and GPP had been measured (Appendix S3, Table A3 and Figure A3). Sites were not included if either variable had been modelled, if GPP and NPP estimates were not independent, or if NPP included only biomass increment and not turnover. Climate data (mean annual precipitation, temperature and radiation) were provided for some sites in the references, but if this was not available, data were extracted for the site latitude and longitude from the 10 min grid cell global climate data provided by the Climatic Research Unit, University of East Anglia, UK, and these parameters are described in Table 2.

Step 3: site data of GPP

A spatial data layer of GPP (mol CO_2 m^2 yr^{-1}) (see Table 2 for definitions of symbols and Appendix S4 for further details) for the southeast Australian region was generated from a 5-year time series (July 2000 to June 2005) of MODIS 16-Day L3 Global 250m (MOD13Q1) satellite imagery using the simplified light-use efficiency model of GPP as formulated by Roderick *et al*. (2001). We calculated GPP for each calendar month and then computed annual sums of GPP for the 5 years commencing in July 2000. For many grid cells, there was little between-year variation in GPP because the vegetation canopy is mostly comprised of evergreen trees and shrubs that maintain a nearly constant leaf area. However, an extensive area within our study region was burnt by intense wildfire in January 2003 and this resulted in a temporary loss of canopy cover, while the carbon stock of the stems, branches, and roots largely remained intact. Consequently, we elected to use the annual maximum GPP calculated for each grid cell for the 5-year study period instead of the mean values as input to our models.

Step 4: environmental variables

Estimates of environmental variables were generated from national spatial geographic information systems for each of the 284 sites. The variables, their symbols, units and source of the information are listed in Table 2. Variables included precipitation, temperature, radiation, water availability index and soil depth, and factors included forest type (two levels), geology (four levels), and topographic position (five levels). A water availability index (W) was calculated from precipitation and radiation to provide an ecologically meaningful expression of the interaction between precipitation and evaporation in relation to vegetation productivity (formula in Table 2). Negative values mean that there is greater potential evaporation than precipitation, hence the water deficit. The spatial resolution of all GIS datasets was converted to $250\,\mathrm{m} \times 250\,\mathrm{m}$ pixels to conform to the MODIS data.

Statistical analysis

Relationships between carbon stocks and NPP with environmental variables were investigated using multiple regression modelling (Payne *et al*., 2003). A logarithmic transformation was applied to homogenize the variance of the residuals (Zar, 1984). Models are presented with the coefficients, standard errors, level of significance ($F_{\mathrm{pr}} < 0.05$) and variance accounted. These models allow carbon stocks and fluxes to be predicted from spatial data, thus enabling up-scaling from site data to regional spatial coverage.

Comparison with national and international carbon accounting systems

The IPCC recommends default values for estimating carbon stocks and fluxes in the world's major biomes in the absence of local data (IPCC, 2003, 2006). Total biomass carbon stock for biomes (defined in table 4.5 and table 3A.5.2, IPCC, 2006) was calculated from aboveground biomass averaged across continents for each ecological zone (table 4.7, IPCC, 2006), carbon fraction in aboveground biomass (table 4.3, IPCC, 2006), ratio of below-to-aboveground biomass (table 4.4, IPCC, 2006), litter carbon stocks (table 3.2.1, IPCC, 2003) and dead wood stocks (table 3.3.3, IPCC, 2003). Biomass carbon stocks were calculated using these default values for the appropriate biomes within the southeast Australian natural eucalypt forest region.

Carbon stocks at each of our field sites were also calculated using the Australian National Carbon Accounting System (NCAS, DCC, 2005). Latitude, longitude, and vegetation type for each site were entered and the model calculated biomass carbon stock using default calibrations that define a biomass productivity surface for the continent.

Results

Results of this study consist of derivation of model parameters to predict spatially the input to dynamic carbon models of NPP and the output of TEC that are required for calibration through model inversion. The process of up-scaling to spatially extend site data to a region is demonstrated for the case study region of eucalypt forests in southeastern Australia.

Step 5. model of NPP – carbon model input

The ratio of NPP : GPP from the global site values (Table A3 and Figure A3) was highly variable (range 0.29–0.61) and nonlinear with respect to GPP. We applied a multiple regression analysis of the global database to predict NPP : GPP from climate variables estimated for each site, which are ecologically relevant to biomass production, yielding the following equation:

$$\mathrm{NPP} : \mathrm{GPP} = a + b_1 \ln T_{global} + b_2 \ln W_{pos} + b_3 \ln Q_{\mathrm{s}\_global}, \quad (3)$$

where symbols are defined in Table 2 and model parameters given in Table 3. Climate variables have been defined as *global* because they are derived from a global spatial dataset, to distinguish this from the regionally derived variables. The model accounted for 51% of the variance and the model estimates are shown in Fig. 4. Thus, the model prediction was $\sim$50% better than the expected fit using a constant ratio or random points between the minimum and maximum of the data range. There was no significant effect of site data from northern or southern hemisphere on the model.

Site-specific climate data for the 284 case study sites in southeastern Australia were extracted from the ANUCLIM climate spatial database (Table 2). Site NPP : GPP ratios were then calculated using Equation 3. Spatial distribution of NPP : GPP over southeastern

Table 3 Regression model coefficients (a, b_1, b_2, b_3) for NPP:GPP, standard errors (SE), and level of significance (F_{pr})

	a	b_1	b_2	b_3
Coefficient	−11.20	2.326	−0.0697	−0.1071
SE	3.33	0.640	0.0390	0.0677
F_{pr}		<0.001	0.002	0.127

NPP : GPP = $a + b_1$ Ln $T_{global} + b_2$ Ln $W_{pos} + b_3$ Ln Q_{s_global}. Variance accounted for is 51%.

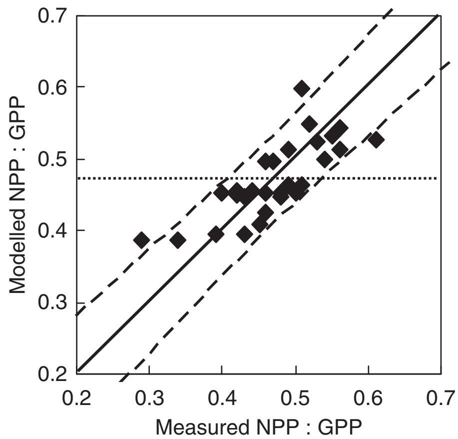

Fig. 4 Measured global site values of [gross and net primary productivity (GPP and NPP)] NPP : GPP compared with the modelled NPP : GPP derived from an empirical model of GPP and climate variables that accounted for 51.5% of the variance. The solid line is the 1 : 1 line, the dashed lines represent the 95% confidence interval of the model, and the horizontal dotted line is the default value commonly used as a constant NPP : GPP ratio.

Australia was calculated for every grid cell giving a range of 0.42–0.60. Using these spatial data for NPP : GPP and GPP (from step 3) the spatial distribution of NPP was calculated, which had a range from 5 to 18 $\mathrm{t\,C\,ha^{-1}\,yr^{-1}}$ across the study region (Fig. 5a). The frequency distribution of NPP by area (Fig. 5b) shows the mean distribution and the shift in distribution with the 95% confidence limits that demonstrates the range in uncertainty.

Step 6: model of TEC – carbon model output

Site data of biomass carbon stocks [from step 1(iv)] were combined with site-specific estimates of NPP [step 5(ii)] and environmental data [step 4(ii)] to derive a multiple regression model to predict living biomass carbon stock and total (living plus dead) biomass carbon stock, in the form of the following equation:

$$\mathrm{Ln(Biomass)} = a + b_1 NPP + b_2 W + b_3 P + b_4 Sd_{AB} + b_5 T\ (\mathrm{t\,C\,ha^{-1}}). \quad (4)$$

The model accounted for 51.4% of the variance for living biomass and 47.7% for total biomass (living plus dead) carbon stocks. Regression model parameters are listed in Table 4 and the relationship between measured and modelled total biomass is shown in Fig. 6. Values of the regression constant a were specific to each factorial combination of vegetation, geology, and topographic position class (factors and classes given in Table 2). Values of the coefficient b_2 for parameter W were specific for combinations of vegetation and topographic position class. Coefficients for each factor class are given in Appendix S5. Sites with highest biomass carbon stock occurred in tall eucalypt forest type (MVG 2) on mid and lower slopes.

The interactions involved in this complex model can be revealed by investigating relationships between individual variables. The relationship between NPP (modelled value from step 5) and biomass carbon stocks (measured value from step 1) for all the sites is shown in Fig. 7. The relationship was not a monotonically increasing response, rather, maximum carbon stock values were evident at mid-values of NPP, and for a given value of NPP there was a wide scatter of biomass values. Sites with the highest total biomass (living plus dead) carbon stocks (mean of 1100 $\mathrm{t\,C\,ha^{-1}}$) were the *Eucalyptus regnans* (F. Muell., Mountain Ash) forests in the Central Highlands of Victoria. These are cool moist temperate evergreen forests with a eucalypt overstorey and dense *Acacia* sp. and rainforest tree understorey (dominated by *Nothofagus cunninghamii* (Hook., Myrtle Beech). Environmental conditions are conducive to plant growth and accumulation of biomass, with high rainfall, moderate temperatures, relatively fertile and deep soils, and a rugged topography that provides many sheltered sites. Highest biomass occurred in stands with two or three age cohorts of overstorey trees and rejuvenated understorey trees, which resulted from partial stand-replacing wildfires (Keith *et al.*, 2009).

Forest types where biomass was relatively low for a high NPP occurred in the subtropics of northern coastal NSW and southern Queensland, where tree longevity was lower and decomposition rates were higher than in cool moist temperate forests, resulting in lower accumulation of living and dead biomass. Sites with limiting environmental conditions, such as low water availability and infertile or shallow soils, had lower biomass for a given NPP. Additionally, some forest stands may not have been at maximum age and hence biomass

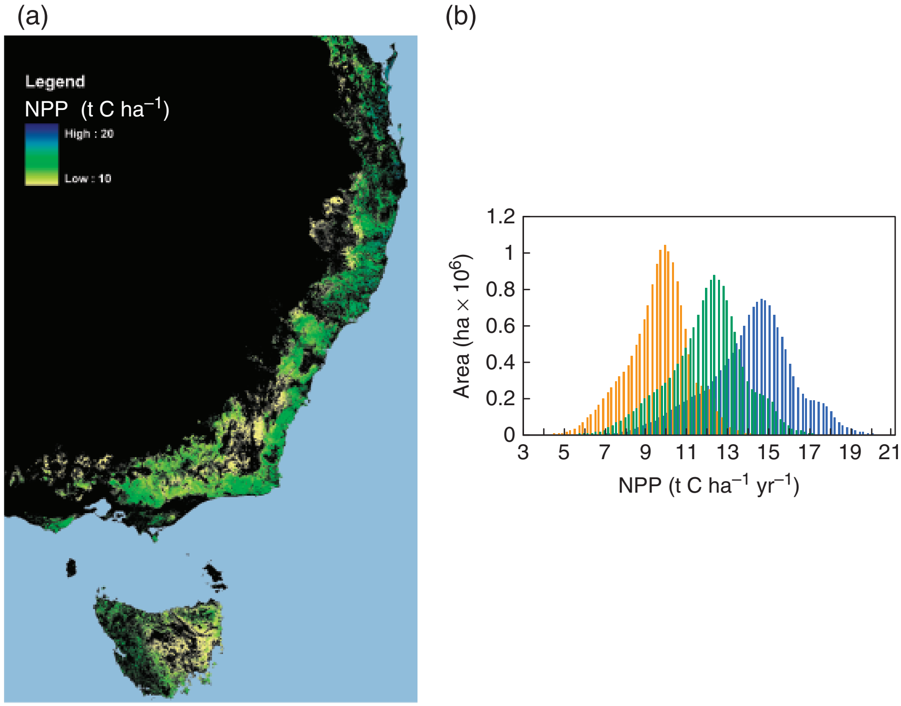

Fig. 5 (a) Spatial distribution of net primary productivity (NPP) in southeast Australia predicted from the model derived from a function of gross primary productivity (GPP) and climate variables. (b) Frequency distribution of NPP by area shown as a histogram with a range from 5 to 18 t C ha^{-1} yr^{-1} for the mean value (green), 4 to 14 t C ha^{-1} yr^{-1} for the lower 95% confidence limit (orange), and 7 to 21 t C ha^{-1} yr^{-1} for the upper 95% confidence limit (blue).

Table 4 Regression model coefficients for total (living plus dead) and living biomass (tC ha^{-1}) with standard errors (SE) and level of significance (F_p)

	a	b_1	b_2	b_3	b_4	b_5
Total biomass						
Coefficient	9.10	0.222	0.0022	−0.0015	−0.362	−0.059
SE	1.81	0.043	0.00097	0.00055	0.157	0.026
F_{pr}		<0.001	<0.001	<0.001	0.01	0.008
Living biomass						
Coefficient	8.28	0.21	0.0014	−0.0018	−0.406	−0.0495
SE	1.82	0.044	0.00098	0.00055	0.158	0.0267
F_{pr}		<0.001	<0.001	<0.001	0.004	0.021

Ln Biomass $= a + b_1$ NPP $+ b_2\ W + b_3\ P + b_4\ Sd_{AB} + b_5\ T$.
Variance accounted for is 47.7% for total biomass and 51.4% for living biomass.
Coefficients for the combinations of factor classes for a and b_2 are given in Appendix S5.

accumulation because, for example, the site land-use or disturbance history was uncertain.

Distribution of sites within the climatic domain of the study area is shown in Fig. 8. The climatic domain was defined by the water availability index (W, derived from precipitation and solar radiation as defined in Table 2) and mean annual temperature (T) within the area occupied by tall (NVIS MVG 2) or open (NVIS MVG 3) eucalypt forest (Fig. 3). These points were calculated from the 5 km resolution ANUCLIM climate spatial database. Areas within the climate envelope that are not mapped as forest could be areas originally forested that have been cleared or converted to plantations, areas that support noneucalypt forest types or woodland, or areas not suitable for forest for some other reason such as edaphic conditions. In Fig. 8, sites are classified by eight regions within southeastern Australia. This distribution of sites illustrates the representativeness of the site data in relation to the study area over which carbon stocks were estimated. Areas poorly represented by site data include cool and wet conditions as occur in Tasmania, and hot and dry conditions as occur in open forest on the west of the Great Dividing Range.

Variation in site total biomass carbon stocks was described in T–W space to illustrate the effect of interactions among these variables (Fig. 9). The positive relationship between biomass carbon stock with W and T is in the form of a curved plane, with the highest biomass occurring in wet and moderately warm conditions. Biomass values below this plane represent sites with suboptimal W for a given T. Sites in the Central Highlands of Victoria have the highest biomass and lie

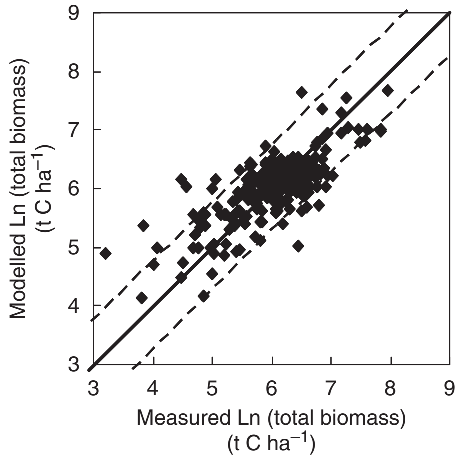

Fig. 6 Measured site values of total biomass (living plus dead) carbon ($t\,C\,ha^{-1}$) compared with the modelled values derived from an empirical model of NPP and environmental variables that accounted for 47.7% of the variance. The solid line is the 1 : 1 line and the dashed lines represent the 95% confidence interval of the model.

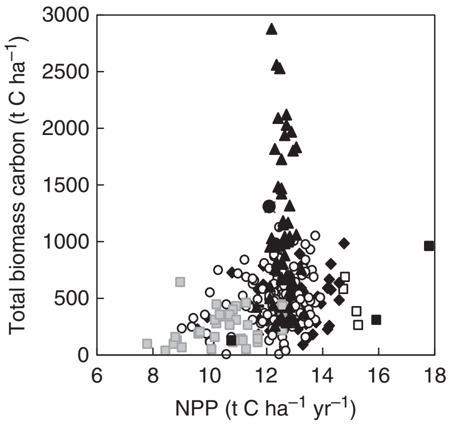

Fig. 7 Site data in southeast Australia ($n = 284$) showing the relationship between total biomass (living plus dead) carbon (measured values from step 1) and NPP (modelled value from step 5). Symbols represent different regions: (◆) south coast NSW, (○) Gippsland, (□) north coast NSW, (–) tablelands, (●) Tasmania, (■) montane, (■) Queensland, (▲) Central Highlands Victoria.

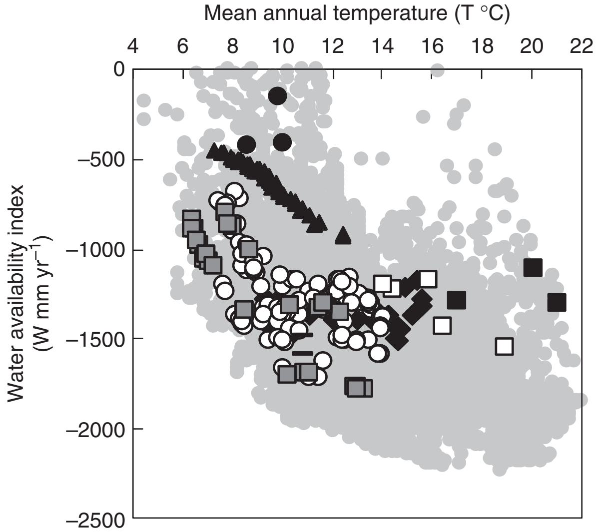

Fig. 8 Distribution of sites within the climatic domain of mean annual temperature and water availability index (greater magnitude of negative *W* represents lower water availability), where symbols represent different regions: (◆) south coast NSW, (○) Gippsland, (□) north coast NSW, (–) tablelands, (●) Tasmania, (■) montane, (■) Queensland, (▲) Central Highlands Victoria. The case study area of eucalypt forests (NVIS MVGs 2 and 3) within southeast Australia is shown as (●) calculated from the 5 km ESOCLIM grid cells of climate variables.

along a *T*–*W* gradient related to their topographic position within a catchment. Sites in Tasmania had higher *W* but lower *T*, and hence lower biomass. In our dataset of eucalypt forests, there were no sites with high *T* and high *W*. Under these conditions eucalypts are replaced by tropical rainforest taxa.

The distribution of carbon stocks among size classes of trees within forest stands (from the measured site data in step 1) is illustrated in Fig. 10. This represents an average of the site data across southeast Australia ($n = 284$). The size distribution differs for carbon stocks and number of trees. Sixty percent of the carbon stock occurs in trees having DBH > 100 cm, but this represents only 4% of the number of trees. Whereas, 60% of the number of trees have DBH < 40 cm and this represents only 10% of the carbon stock.

Step 7: spatial distribution of carbon stocks

The spatial distribution of carbon stocks across the study area is shown in Fig. 11a, based on landscape scale variation in environmental conditions calculated from the model in Table 4. Total carbon stocks of components are summarized in Table 5. The frequency distribution of carbon stocks by area (Fig. 11b) shows the mean distribution and the shift in distribution with the 95% confidence limits that demonstrates the range in uncertainty. The total area integrated under the curves remains the same at 14.5 million ha of forest, but the confidence limits show the range in biomass density with the lower limit having a higher proportion of area with low biomass density, and the upper limit having a higher proportion of area with high biomass density. Note that predictions of total biomass carbon stocks at CCC were generated for eucalypt forests in the study area across all land tenures irrespective of land-use history. The extant forest consists of stands of

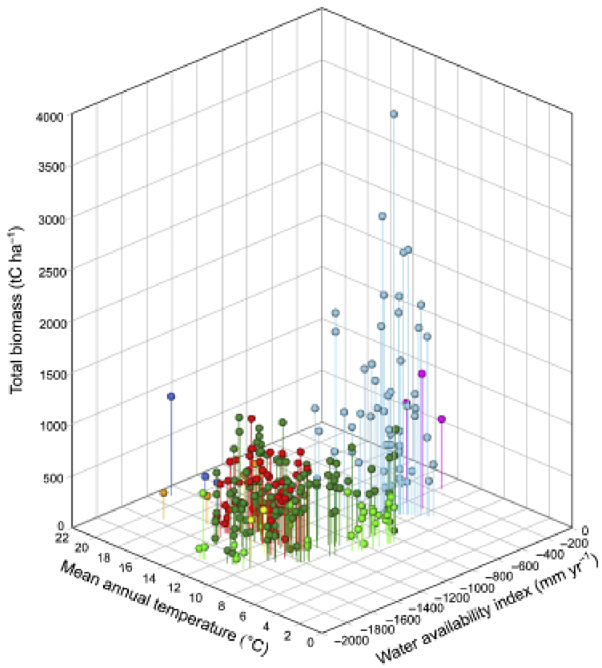

Fig. 9 Spatial variation in total biomass (living plus dead) carbon at each site ($n = 284$) shown in the climatic domain of mean annual temperature and the water availability index (greater magnitude of negative W represents lower water availability). Sites are categorized by region: south coast NSW (red), Gippsland (green), north coast NSW (orange), tablelands (yellow), Tasmania (magenta), montane (lime green), Southern Queensland (dark blue), Central Highlands Victoria (light blue).

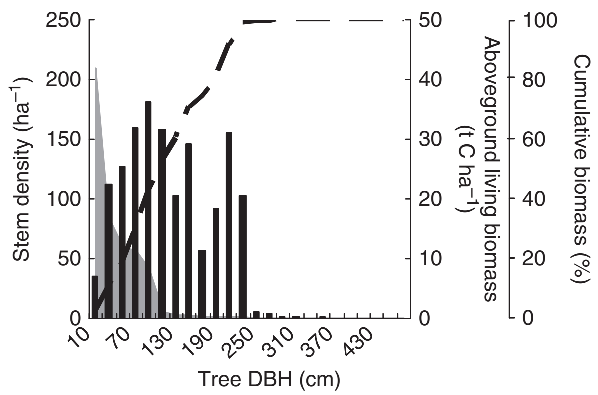

Fig. 10 Size class distribution of trees averaged across all sites measured in the case study of southeast Australia ($n = 284$). The carbon stocks in aboveground living biomass in each size class are shown as the black bars, the cumulative biomass as the dashed black line, and the number of trees as the grey area. Tree DBH represents the mid-point of the 20 cm size class.

varying ages whose current carbon stocks may be well below the predicted CCC.

TEC stock includes biomass and soil carbon. Only a few inventory sites had soil data. For sites with no available field data, soil organic carbon in the A and B horizons (SOC_A and SOC_B) were derived from spatial estimates of soil carbon concentration and bulk density in the Australian Soil Resource Information System (McKenzie *et al*., 2005) (Table 2). The total stock at CCC of the 14.5 million ha of eucalypt forest in southeast Australia was estimated to be approximately 9 Gt C.

Comparison with national and international carbon accounting systems

Our analyses (Table 5) showed that the average stock of total biomass carbon for natural forests in southeast Australia is about 360 t C ha^{-1}, compared with the IPCC default value of 202 t C ha^{-1} for moist temperate forests. Also, our average NPP is 12 t C ha^{-1} yr^{-1} (SD = 1.8) compared with the IPCC default of 7 t C ha^{-1} yr^{-1} (IPCC, 2006). Figure 12 shows the relationship between carbon stock in aboveground living biomass and water availability at each of our field sites ($n = 284$) by comparing (a) the measured site data, (b) biomass calculated using the empirical model described in this paper, and (c) biomass calculated by the Australian National Carbon Accounting System (NCAS).

Discussion

Carbon stocks of eucalypt forests are higher than previously estimated

Carbon stocks of the natural eucalypt forests in the study area, estimated using our empirical model calibrated with site data, are greater than the NCAS (DCC, 2005) estimates for southeast Australia, and IPCC (2003, 2006) estimates for moist temperate forests. There are several possible reasons for the low IPCC estimates. The biome classifications, at the levels of either all temperate forest or warm and cool moist temperate forest, incorporate a wide diversity of forest ecosystem types. These biome-average values probably under-represent evergreen moist temperate forest types, such as the eucalypt forests in southeast Australia (Keith *et al*., 2009). Additionally, the biome-average values may not distinguish adequately forest condition due to land-use history that reduces carbon stocks. The low NCAS estimates most likely reflect the fact that this model was developed for the purpose of assessing carbon stocks in afforestation and reforestation projects under the Kyoto Protocol. Therefore, the focus of NCAS is on simulating growth in younger forests that are influenced by human land-use activity, and is probably poorly calibrated for mature natural eucalypt forests.

Our analyses differ from the previous studies, which have underestimated the carbon stock in natural

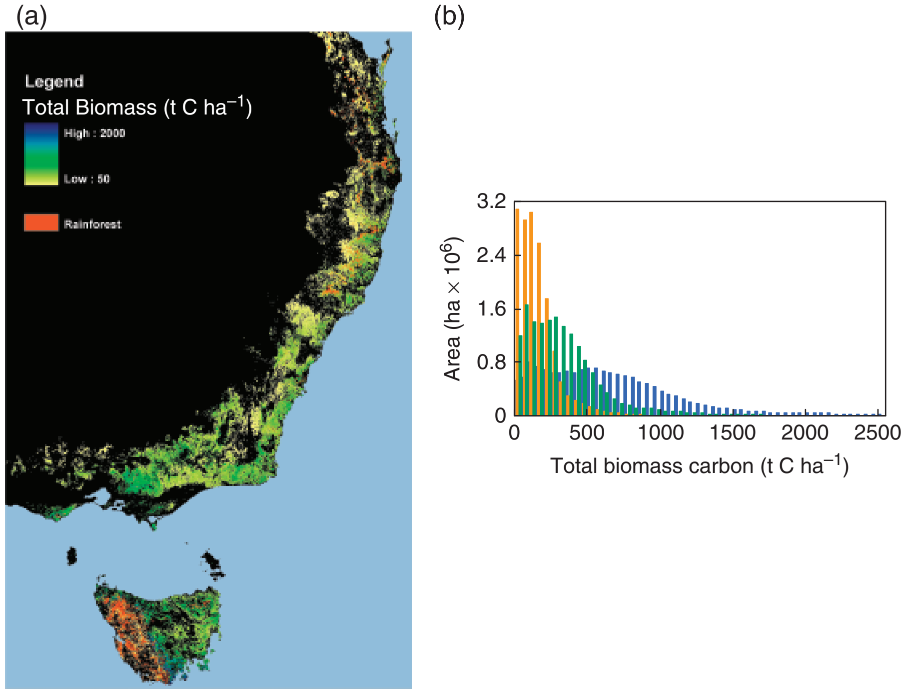

Fig. 11 (a) Spatial distribution of total biomass (living plus dead) carbon in southeast Australia predicted from the model derived from a function of net primary productivity (NPP) and environmental variables. (b) Distribution of total biomass carbon by area shown as a histogram with values of $<50\,\mathrm{t\,C\,ha^{-1}}$ up to $2500\,\mathrm{t\,C\,ha^{-1}}$ in the mean distribution (green), up to $1400\,\mathrm{t\,C\,ha^{-1}}$ in the distribution of the lower 95% confidence limit (yellow), and up to $4500\,\mathrm{t\,C\,ha^{-1}}$ in the distribution of the upper 95% confidence limit (blue) (using a threshold area of 1000 ha).

Table 5 Summary of carbon content in each component of the carbon carrying capacity for the eucalypt forests of southeast Australia covering 14.5 million ha, with a total and mean for the area

Component	Soil	Living biomass	Total biomass (living plus dead)	Total carbon
Total carbon ($\mathrm{tC} \times 10^6$)	4060	4191	5220	9280
Carbon density ($\mathrm{tC\,ha^{-1}}$)	280 (161)	289 (226)	360 (277)	640 (383)

Standard deviations in parentheses represent spatial variability over the region.

eucalypt forests of southeast Australia, primarily because of the manner in which our analyses have addressed the potential sources of error identified in Table 1 (error types 1–7). The following discussion about the issues and means of addressing errors provide some insight into how regional estimates of carbon fluxes and stocks can be improved to provide a more reliable baseline for carbon accounting.

Error type 1: interpretation of variable NPP

Describing and understanding spatial variation in NPP is central to many questions in global change biology because this flux represents energy flow through ecosystems that sustains life, and ecosystem function (Enquist *et al.*, 2003; Zaks *et al.*, 2007). The ratio of NPP : GPP is likely to be conservative because growth, photosynthesis and respiration are strongly linked. However, we suggest that climate, environmental conditions, plant functional type and stand age influence this allocation of energy so that the ratio varies spatially. Empirical and theoretical reasons can be identified to explain this variation.

Empirically, the site data presented in Figure A3 show that the ratio varied from 0.29 to 0.61. Differences in NPP : GPP between tree species morphology have been noted (Ryan *et al.*, 1997; DeLucia *et al.*, 2007), where the ratio was higher for deciduous trees than conifers. This difference was attributed to the greater foliar biomass and respiration in evergreen trees, and lower net stemwood respiration in smooth bark that contains chlorophyll. The

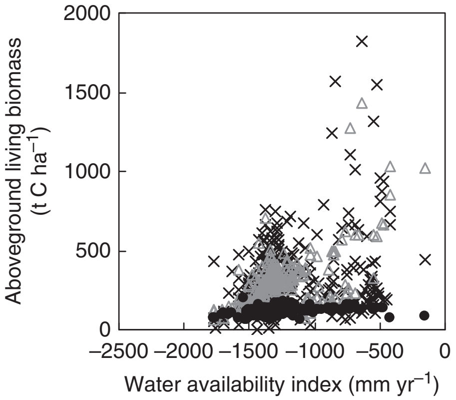

Fig. 12 Relationship between the water availability index and aboveground living biomass carbon and the water availability index (*W*) showing the comparison between (×) measured biomass at field sites, (△) modelled biomass, (●) biomass derived from the Australian National Carbon Accounting System.

ratio has been found to decrease with increasing stand age (Makela & Valentine, 2001; Gifford, 2003; DeLucia *et al*., 2007). Differences among seedlings grown under controlled conditions were found to be related to species, age, plant tissues, and environmental conditions (Gifford, 2003). Additionally, field-grown trees had slightly lower ratios than glasshouse-grown seedlings, suggesting that resource limitation and age produced greater respiratory requirements (Gifford, 2003).

Theoretical reasons for the variation in the NPP : GPP ratio are based on the use of data and understanding of processes of terrestrial carbon cycling. First, the data used by Waring *et al*. (1998) to estimate GPP and NPP and derive a constant ratio, were not independent. In some cases, GPP was estimated indirectly using R_a, and linear relationships were assumed between net biomass production and respiration, which means that a constant relationship was assumed between GPP and NPP in the calculations (Medlyn & Dewar, 1999). Second, the processes of GPP and R_a are influenced differently by environmental conditions, such as temperature, water, and nutrient availability, and so will not necessarily change in the same proportion each year. Third, timing of GPP and R_a processes vary. R_a represents metabolism of stored carbon in plants that is produced over varying time periods not necessarily in a given year, or in the same time period of accounting for GPP (Roxburgh *et al*., 2005; Vargas *et al*., 2009). It is possible for R_a to exceed GPP over a year because stored carbon is being metabolized. Seasonal allocation patterns of assimilate and storage pools of carbohydrate in plants create a lag between substrate production and utilization. A constant ratio approach may be satisfactory when averaged over many years, but not for estimation of NPP in a particular year or season, and it is rare to have flux data for many years to be able to provide a robust average. Fourth, the proportion of carbon uptake used for biomass production and turnover times of biomass components vary in response to climate conditions.

The NPP : GPP ratio is likely to be within a bounded range determined by metabolic efficiency and respiratory costs associated with structural maintenance, nutrient acquisition and transport. There are minimum respiratory costs for growth and maintenance which means the maximum NPP : GPP ratio would be between 0.6 and 0.7. A minimum ratio would be about 0.2 given that there is nearly always some biomass accumulation including litter production, otherwise plants would not survive. The limits determined by these processes suggest an allowable range of NPP : GPP of 0.2–0.65 (Ryan *et al*., 1997; Amthor, 2000) or 0.23–0.83 (DeLucia *et al*., 2007), which coincides reasonably well with the span of available site data (0.29–0.61).

Variation in NPP : GPP is important to take into account for both predicting NPP at sites and also describing the processes controlling production and biomass accumulation (Cannell & Thornley, 2000). An empirical relationship such as presented here (Equation 3) enables NPP to be calculated more accurately, thus improving estimates of carbon cycle components.

Error type 2: conversion of NPP to carbon stock is variable

Our empirical data for NPP and biomass carbon stocks showed that the relationship was not a monotonically increasing response and there was a wide scatter of points. The relationship shown in Fig. 7 indicated that high carbon assimilation can occur that is not necessarily converted into high biomass stocks because accumulation of biomass depends on allocation of biomass components and their turnover rates. High spatial variability reflects the influence of environmental variables and natural disturbance regimes on the residence time of carbon in biomass and soil components. Hotter, wetter environments, in general, have faster turnover rates and hence lower biomass accumulation for a given NPP. The great variability in biomass carbon produced for a given NPP suggests that converting the carbon flux of NPP into a carbon stock of biomass requires the interaction of additional variables that reduce biomass accumulation. Hence, we showed that including a range of environmental variables, together with the input of NPP in an empirical model, improved prediction of biomass carbon by ~50%. The relative importance of environmental variables may vary among regions or biomes depending on the main resources limiting biomass productivity.

Error type 3: adequate sampling of forest type diversity

Adequate sampling of forest type diversity and landscape variability by field site data should mean that the effect of differences in climate, soils, topography, and natural disturbance regimes are reflected in the estimates of carbon stocks. Existing field datasets in southeastern Australia have not been collected explicitly for the purpose of providing representative data of forest types over this region, and therefore we cannot assume that variability in environmental conditions across the landscape and natural disturbances have been sampled adequately by our data. Obtaining representative site data from natural forests presents some difficulties, including the fact that tree ages are often unknown, stands may consist of multiple tree age cohorts, disturbance history of the site may be unknown, and many sites may be inaccessible in rugged terrain. Furthermore, there is often limited information about growth curves for less common and noncommercial species, or about variation in residence times of carbon in living and dead biomass as well as in soil components.

Obtaining representative data for trees within sites is important when measuring inventory plots to provide robust spatial estimates of biomass. First, the full-size range of trees that occur in the forest type must be sampled (where trees are usually considered as those with a diameter $\geq$10 cm). Second, plots must be of sufficient size to sample adequately the size class distribution of trees. Third, plots must be located in a stratified random design that representatively samples different forest types in a nonbiased manner.

Statistical models enable the mean and standard deviation of carbon stocks to be calculated. Where there is some confidence that site data are representative, the standard deviation can be interpreted to reflect natural variability, due to landscape heterogeneity and natural disturbance histories, which affects production of biomass in the region.

Error type 4: site data below CCC

Selection of site data from southeastern Australia for this case study was based on the criterion that forest stands were largely undisturbed by intensive human land-use activity but would have experienced natural disturbances such as fire and insect attacks, and so represented the CCC of the forested landscape. In contrast, sites used in previous estimates, such as NCAS, were often based mainly on regrowth and plantation forests that did not sample large trees; the component where most of the carbon is stored in natural forests. Most available inventory data are from younger forests; characterized by land uses of relevance to the Kyoto Protocol rules for afforestation and reforestation. Methodology and data required for carbon accounting in natural forests differ from that required in plantations and regrowth forests. In addition, total biomass carbon stocks are often underestimated because dead biomass components have not been included. As shown here, dead biomass in the form of litter, CWD and dead standing trees constitutes a large proportion of the total stock in many ecosystems, but is poorly represented in site data or process models.

Error type 5: accuracy of allometric equations

Existing allometric equations for eucalypt species in southeastern Australia probably do not represent adequately the variability in tree form across species and environmental conditions. We made the best possible attempt to use the most appropriate equations, whether site specific or general, for each type of inventory data. Allometric equations derived from harvested trees and biomass measurements were used wherever possible, rather than estimates using stem volume and wood density. Equations have been derived to estimate stem volume of many commercial timber species within the size range harvested, but there is less information about the expansion factors required to incorporate all biomass components, and the amount of decay. Expansion factors and decay are particularly important for large, old trees compared with commercial-sized mature trees. This is because a relatively larger proportion of the biomass is in the branches, and decay is more prevalent. Where stem volume was used in this study it was calculated from individual tree DBH data, however, there is also a lot of data on stem volume per hectare for commercial forests. Use of this stem volume data requires expansion factors that include the non-merchantable species, for example rainforest trees in wet sclerophyll forests that contribute to the high biomass. Our estimates of carbon stocks were conservative because allometric equations were either not extrapolated beyond the size range of trees measured, or an asymptote of maximum biomass was applied. We incorporated reductions due to decay when biomass was estimated from stem volume, and due to noncircular cross-sections of tree bases. Estimating the proportion of decay in large trees under different environmental conditions is an important area requiring further research.

Error type 6: spatial extrapolation of site data

The diversity of species in natural forests, the occurrence of multiaged stands, and heterogeneity in topography and substrates across landscapes, mean that carbon stocks are better estimated as a function of environmental conditions that determine biomass accumulation rather than averages for a forest type and stand age or biome. This has been shown by Baccini *et al*. (2004) and Gibbs *et al*. (2007). Accuracy of the environmental correlations with biomass carbon stocks is limited by the types of environmental data that are available spatially, and the resolution of these data. Areas of research that would improve these spatial estimates include (1) finer spatial scales, as has been done for digital elevation models that provide topographic position (Hutchinson *et al*. 2008), and (2) spatial information about soil properties. Our estimates of carbon stocks were conservative because the spatial extent of estimated carbon stocks was not extrapolated beyond the range of site data.

Error type 7: spatial scales of site and GIS data

In our case study, the grid cell area was $\sim$6 ha while the plot area for the site data ranged from 0.04 to 3 ha. The potential error in relating small plots with larger

Table 6 Summary of sources of error, improvements in uncertainty used in the current study, suggested future improvements and their relative importance

Error type	Improvement in uncertainty by current study	Future research required	Relative importance to improve uncertainty
1. Interpretation of variable NPP	Modelled values of NPP derived from GPP and environmental variables improved estimates by an average of 50%	Experimental research required to provide site data for calibration	Very high
2. Conversion of NPP to carbon stock is variable	Modelled values of biomass carbon stock derived from NPP and environmental variables improved estimates by an average of 50%	Experimental research required to investigate processes controlling longevity of biomass components	High
3. Adequate sampling of forest type diversity	Use of data from undisturbed sites with large trees improved modelled estimates of biomass, as seen by the comparison with NCAS	Synthesis of existing inventory data together with targeted experimental work to fill gaps, particularly measurements of large trees and forest types in reserves	Moderate
4. Site data below CCC	Use of data from undisturbed sites with large trees improved modelled estimates of biomass, as seen by the comparison with NCAS	Information about land use history and the effect on degradation of carbon stocks is required	Very high
5. Accuracy of allometric equations	Tree biomass estimates improved by applying a few equations derived from larger trees, and incorporating reductions due to wood decay	Need for biomass measurements of large trees, proportions of decay, and changes in wood density with age of trees	High
6. Spatial extrapolation of site data	Spatial extrapolation of biomass density based on environmental variables is more accurate than forest type averages	Improvements required in estimating environmental variables functionally related to biomass accumulation. Site data is required on soil carbon in natural forest ecosystems and relationships with environmental variables to allow spatial scaling	Moderate for biomass Very high for soil carbon
7. Spatial scales of site and GIS data	Existing site data was used of variable plot sizes	Experimental work required to fill gaps in biomass data should include plot inventories at the scale of remote sensing grid cells	Moderate

CCC, carbon carrying capacity; GIS, geographic information system; NPP, net primary productivity.

grid cells is due to the fact that the plots may not be representative of the larger area. The need to use existing data cannot overcome this problem, but future site data surveys should aim to better match the resolution and location of remote sensing and GIS data.

We summarize methods employed in the current study and future research required for improving uncertainty in each of the seven error types in Table 6.

Conclusions

We have identified methods to improve carbon accounting in natural forests using appropriate calibration with ecological data from field sites with minimal human disturbance. Calculating the CCC with methods inclusive of spatially variable NPP in relation to environmental conditions provides more reliable spatial estimates of carbon accounts than forest type average values. The efficacy of these empirical models is highly dependent on the quality of the input data, including the extent to which the field data are representative of landscape heterogeneity of natural forests and whether land-use history has been taken into account.

CCC is the most appropriate baseline to use for carbon accounting in landscapes dominated by natural forests, and can provide a basis for monitoring land-use activities or changes in land management that result in either depletion of carbon stocks or an increase due to forest growth. Improvement of the empirical derivation of NPP presented here should be a continuing focus of research as better calibrated descriptions of ecophysiological processes are needed in simulation models to calculate NPP.

Providing accurate estimates of carbon stocks in natural forest ecosystems is important so that they are factored into economic valuations and policy options for climate change mitigation. Existing carbon accounting and default values that underestimate carbon stocks in natural forests may result in underestimation of the depletion of carbon stocks and associated CO_2 emissions due to human activities. Potential for sequestration of carbon by forest growth also may be underestimated. More reliable estimates of baseline carbon stocks, such as the CCC defined here, will improve understanding of the contribution of natural forests to the global carbon cycle.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Estimation of tree biomass.
Appendix S2. Site carbon stock database for southeast Australia.
Appendix S3. Global site data for NPP:GPP.
Appendix S4. Method for calculation of Gross Primary Productivity over the southeast Australia case study region.
Appendix S5. Biomass carbon model coefficients.

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