Glacial Amazonia at the canopy-scale: Using a biophysical model to understand forest robustness

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ABSTRACT

A canopy-scale model (CANOAK) was used to simulate lowland Amazonia during the Last Glacial Maximum. Modeled values of Net Ecosystem Exchange driven by glacial environmental conditions were roughly half the magnitude of modern fluxes. Factorial experiments reveal lowered [CO_2] to be the primary cause of reduced carbon fluxes while lowered air temperatures enhance net carbon uptake. LGM temperatures are suggested to be closer to optimal for carbon uptake than modern temperatures, explained through the canopy energy balance. Further analysis of the canopy energy balance and resultant leaf temperature regime provide viable mechanisms to explain enhanced carbon-water relations at lowered temperatures and forest robustness over glaciations. An ecophysiological phenomena known as the 'cross-over' point, wherein leaf temperatures sink below air temperature, was reproduced and found to demarcate critical changes in energy balance partitioning.

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1. Introduction

A sizable body of palynological and palaeovegetative modeling studies provide a justifiable estimate of lowland Amazonian palaeoecology over glacial-interglacial cycles. Pollen records have determined Pleistocene floristic composition and corresponding palaeoclimates, providing grounds to reconstruct past biome distributions and characteristics (Bush et al., 2004) (Burbridge et al., 2004) (Haberle and Maslin, 1999) (Mayle et al., 2000) (Oliveira, 1992). Unfortunately, complete pollen records in the Amazonian lowlands that date back to the Last Glacial Maximum (LGM) are scarce and large-scale inferences must be made from a limited data set (Mayle et al., 2009). To compliment these empirical efforts, modelers have applied several process-based, regional scale models to answer similar questions while searching for underlying ecological mechanisms and feedbacks (Marchant et al., 2004) (Marchant et al., 2006) (Beerling and Mayle, 2006) (Cowling et al., 2001). Synthesis of these two independent approaches has been fruitful but we are still far from a complete understanding of past climatic changes and ecological responses in Amazonia.

The current consensus is that Amazonian forests retained a closed-canopy over glaciations, refuting Haffer's Refugia Hypothesis that proposed dramatic biome fragmentation and the formation of savanna-enclosed patches of moist forest (Haffer, 1969). This theory is consistent with both pollen records from lowland ever-green forest and the Amazon fan, as well as regional modeling studies (Bush and Oliveira, 2006) (Colinvaux et al., 2000) (Cowling et al., 2001) (Marchant et al., 2004). The simulated maintenance of forest cover was proposed to originate in improved carbon-water relations correlated with cooler air temperatures, allowing continued dominance of forests against encroaching grasslands.

There is, however, evidence of expanded savannah in marginal regions of Amazonia despite general forest robustness, suggesting limits to the effects of enhanced carbon-water relations (Burbridge et al., 2004) (Mayle et al., 2000). The carbon storage of glacial forests has also been suggested to have been significantly lower (∼ 50%) than that of pre-Industrial Amazonia (Beerling and Mayle, 2006). Cowling also found glacial forest canopy density to be lower and more heterogeneous than that of modern lowland forests, attributing these differences to low atmospheric carbon dioxide rather than temperature or aridity. Conversely, at more extreme values, lower air temperature can also diminish forest cover as

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deduced by studies on Andean sites of much higher elevation (Mourguiart and Ledru, 2003). A motivation for our study is to develop a more comprehensive and quantitative foundation behind these processes.

After determining *what* happened to Amazonian forests during climatic change, it is our intention to address *how* and *why* it happened. To do this, we investigate the specific ecological processes that can account for the larger scale changes that comprise our current picture of Pleistocene Amazonia over glacial-interglacial cycles. Our tool of choice is a canopy-scale model (CANOAK), built to capture and quantify finer scale phenomena outside the scope of previous studies. This approach puts a greater emphasis on ecophysiology, the study of an ecosystem and its components' physiological interactions with the environment, which connects closely with modern forestry and carbon modeling. With this method, we can also explore the broader implications of these ecosystem processes, connecting to topics such as biome stability, drivers of biodiversity, and the projection into the future of Amazonia.

2. Methods

2.1. Canopy model

CANOAK is a canopy-scale biophysical model developed by Dennis Baldocchi that computes carbon, water, and energy exchange (fluxes) between the biosphere and atmosphere, integrating concepts from micrometeorology, biochemistry, and ecophysiology. It has been grounded and applied to a number of field sites against measured fluxes (eddy covariance systems) over a range of timescales, predominantly in temperate regions (Baldocchi and Harley, 1995) (Baldocchi, 1997) (Baldocchi and Meyers, 1998) (Baldocchi and Wilson, 2001). Rigorous validation of CANOAK against flux measurements suggests that modelers are correctly parameterizing ecosystem processes while indicating phenomena unaccounted for by the model. While plant physiology has evolved significantly, it is likely that the processes simulated are valid in palaeoecological settings or conversely, can suggest specific evolutionary adaptations that may have occurred to confound our assumptions.

The model is driven by meteorological data in hourly steps (air temperature, [CO$_2$], incoming radiation, etc.), simulates radiative transport through the canopy, to then compute the energy balance through multiple layers of leaf and soil to estimate fluxes of sensible and latent heat (Paw, 1987). This also determines proportions of 'sunlit' and 'shaded' leaves and their respective leaf temperature profiles. A key ecosystem parametrization used in this study that is neglected in regional studies is the encoding of vertical resolution within the canopy, which has been shown to significantly improve the fidelity of computed fluxes (Smith et al., 2010). A simplified flow of processes used by CANOAK is shown in Fig. 1, based on a version by Baldocchi and Wilson (2001).

The Farquhar model for photosynthesis (eq. (1) and (2)) (Farquhar et al., 1980) was used in combination with the Ball-Berry-Collatz model for stomatal regulation (eq. (3)) (Collatz et al., 1991):

$$A = V_c - 0.5V_o - R_d, \tag{1}$$

$$V_c - 0.5V_o = \min(W_c, W_j)(1 - \Gamma/C_i), \tag{2}$$

where A is the rate of photosynthesis, V_c is the rate of carboxylation, V_o is the rate of oxygenation, and R_d is the rate of dark respiration. In eq. (2), min (W_c, W_j) is the minimum between W_c, the rate of carboxylation when Ribulose Biphosphate (RuBP) is saturated and
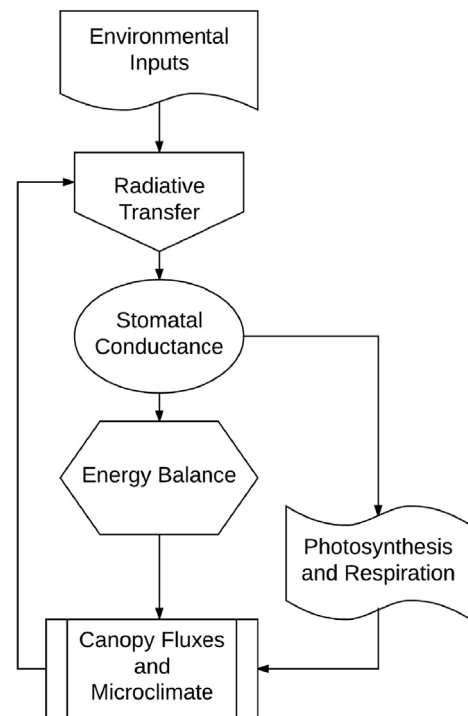

Fig. 1. Flow of submodules used by CANOAK to compute carbon, energy, and micro-climatic profiles.

W_j, the rate of carboxylation when limited by electron transport (low light conditions). The compensation point (Γ) is the CO$_2$ mole fraction where carbon uptake equals carbon loss, and C$_i$ is the intercellular CO$_2$ mole fraction.

Stomatal conductance (g$_s$) can be expressed as a linear function of photosynthesis (A) through eq. (3), for a given relative humidity (rh). The parameters m and g$_0$ are the respective slope and intercept that are fitted against leaf-level gas exchange experiments (Collatz et al., 1991).

$$g_s = mArh/C_s + g_0 \tag{3}$$

The system of equations coupling photosynthesis and stomatal conductance was embedded in a cubic equation and solved analytically within CANOAK (Baldocchi, 1994).

Photosynthesis, respiration, and transpiration are calculated for each leaf layer and then summed for net ecosystem exchanges (Baldocchi, 1994). This computational flow is iterated for each time step until stable values of microclimate, carbon and energy fluxes are reached. Soil and bole respiration are treated using empirical functions while intra-canopy mixing is driven by a turbulent transfer submodule. Soil respiration was set to a constant rate of 6 μmol/m^2 s based on recent studies of similar sites (Luo and Zhou, 2006) (Adachi et al., 2009). Comprehensive descriptions of the model and its underlying theory can be found in (Baldocchi and Meyers, 1998) (Baldocchi et al., 2002) (Monson and Baldocchi, 2014).

A central concept used in this study is the canopy energy balance (Paw, 1987). The energy balance of an ecosystem describes the flows of incoming, outgoing, and stored energy, serving as the interface between the environment and the surface, which in this case is a forest canopy. Solar radiation drives this system and is either reflected, transmitted, or absorbed, depending on the canopy's spectral properties. Whatever is absorbed is then partitioned into latent heat (evapotranspiration), sensible heat (advection), or