



Testing quantitative pollen dispersal models in animal-pollinated vegetation mosaics: An example from temperate Tasmania, Australia



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ABSTRACT

Reconstructing past vegetation abundance and land-cover changes through time has important implications in land management and climate modelling. To date palaeovegetation reconstructions in Australia have been limited to qualitative or semi-quantitative inferences from pollen data. Testing pollen dispersal models constitutes a crucial step in developing quantitative past vegetation and land cover reconstructions. Thus far, the application of quantitative pollen dispersal models has been restricted to regions dominated by wind-pollinated plants (e.g. Europe) and their performance in a landscape dominated by animal-pollinated plant taxa is still unexplored. Here we test, for the first time in Australia, two well-known pollen dispersal models to assess their performance in the wind- and animal-pollinated vegetation mosaics of western Tasmania. We focus on a mix of wind- (6 taxa) and animal- (7 taxa) pollinated species that comprise the most common pollen types and key representatives of the dominant vegetation formations. Pollen Productivity Estimates and Relevant Source Area of Pollen obtained using Lagrangian Stochastic turbulent simulations appear to be more realistic when compared to the results from the widely used Gaussian Plume Model.

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1. Introduction

The development of realistic estimates of vegetation and land cover change from sub-fossil pollen data is crucial for attempts to both understand how vegetation responds to factors such as climatic change and disturbance. Terrestrial vegetation is an important component of the Earth System that is both influenced by climate and influences climate through biogeochemical and biogeophysical processes/feedbacks (e.g. Foley et al., 2003). Indeed, recognition of this mutual influence has led to the coupling of dynamic vegetation models (DVMs) with climate models (e.g. Smith et al., 2011) and fire models (Thonicke et al., 2001) in an attempt to better model Earth System dynamics. Critically, DVMs coupled with climate and fire models only simulate climate-induced potential vegetation and do not take account actual past land-cover changes (Smith et al., 2011; Thonicke et al., 2001). Thus, it stands that the development of quantitative land-cover estimates through

time is of critical importance for improving models' performance (Strandberg et al., 2014; Trondman et al., 2015).

Pollen data are often times dramatically skewed in favour of a few abundant pollen types, a fact that has hampered quantitative vegetation reconstruction since the beginning of the palynological research (von Post, 1946). This gap in our understanding not only prevents attempts to fully understand how vegetation systems respond to environmental change, it runs the risk of mismanagement of ecosystems whose baseline variability is poorly known. Not until the most recent decade have increased computer power, reduced analysis time and the compilation of large pollen datasets conspired to allow the development of robust quantitative techniques suitable for Quaternary pollen data (Sugita, 2007a,b; Gaillard et al., 2010). Application of these cutting-edge advancements is largely restricted to Europe and North America (e.g. Sugita et al., 1999; Broström et al., 2004; Bunting et al., 2005; Räsänen et al., 2007; Soepboer et al., 2007, 2008; Filipova-Marinova et al., 2010; Poska et al., 2011; Abraham and Kozáková, 2012; Hjelle and Sugita, 2012; Li et al., 2015), with virtually no attempts at applying these approaches in the Southern Hemisphere (Duffin and Bunting, 2008). The first step toward generating robust estimates of

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vegetation from pollen data is the development of suitable pollen dispersal models (e.g. Theuerkauf et al., 2013). Here we test empirical pollen dispersal models in western Tasmania, Australia, a region that substantially differs from the models' previous applications in the Northern Hemisphere because of the abundance of animal-pollinated plant taxa in the vegetation canopy.

The Landscape Reconstruction Algorithm (LRA) (Sugita, 2007a,b), developed in Europe, represents the state-of-the-art model for generating quantitative land cover estimates from pollen data. The LRA is underpinned by pollen dispersal models developed, to date, principally from Northern Hemisphere plants that are assumed to be largely wind-dispersed, especially canopy trees from the Betulaceae, Fagaceae and Pinaceae families (Tauber, 1965; Andersen, 1970, 1974; Andersen, 1974; Prentice, 1985; Sugita, 1993, 1994, 2007a,b; Calcote, 1995). The assumption of wind-dispersal from the canopy is a critical limitation that restricts the application of the Landscape Reconstruction Algorithm to vegetation types dominated by wind-dispersed canopy species. In landscapes with animal-mediated pollination, the applicability of these models for vegetation reconstruction is unknown and has been questioned (Walker, 2000; Duffin and Bunting, 2008).

In Australia, the most important canopy dominants (e.g. *Eucalyptus*, *Acacia*, *Melaleuca*) are pollinated by insects, marsupials, birds, insects and bats (zoophilous pollination) (Andersen, 1970; Kershaw and Strickland, 1990). The lack of quantitative information about pollen dispersal parameters of these taxa constitutes a significant knowledge gap. While the limited application of semi-quantitative techniques in Australian palynology has allowed objective inferences of vegetation change from pollen data (e.g. Kershaw, 1979; Fletcher and Thomas, 2010a,b), the lack of truly quantitative approaches to vegetation reconstruction severely limits the understanding of long-term vegetation change in this region. A case-in-point is the long-standing debate over if and when moorland replaced rainforest in western Tasmania during the mid to late Holocene (Thomas, 1995; Colhoun, 1996; Fletcher and Thomas, 2010a,b; Thomas et al., 2010; Macphail, 2010). Despite dominating the landscape, moorland vegetation is virtually invisible in the pollen spectra (Fletcher and Thomas, 2007). Indeed, over-representation of anemophilous rainforest taxa in pollen spectra has led to the routine ignorance of the existence of treeless vegetation in this landscape (Colhoun, 1996; Pickett et al., 2004; Colhoun and Shimeld, 2012) and there is a need to quantitatively address the biases inherent in pollen data to better understand long term vegetation dynamics in landscapes such as this.

In this paper, we aim to test, for the first time in Australia, the application of pollen dispersal models in order to quantify past land-cover changes in western Tasmania, Australia. Specifically, we test two of the leading dispersal models, the Gaussian Plume Model (GPM) and the Lagrangian Stochastic Model (LSM), to assess their performance in a landscape dominated by animal- and insect-pollinated plant taxa, a mix that differs substantially from the vegetation in which they were developed. Testing these models has important implications for 1) extending the geographical scope of quantitative land-cover reconstructions to the Southern Hemisphere and to areas which have been previously ignored because of the abundance of animal-pollinated plant taxa and 2) providing an objective test of competing theories of Holocene landscape evolution in such areas (e.g. Tasmania).

2. Pollen dispersal, production and relevant source area

Pollen dispersal is one of the major factors in determining the representation of vegetation in pollen spectra, along with taphonomy, pollen productivity and pollination mode (Faegri and Iversen, 1989). These issues often result in a non-linear

relationship between pollen percentages and vegetation cover (e.g. Gaillard et al., 2010). Pollen productivity varies among species depending on biological and ecological parameters such as their pollination system, plant life forms, flower traits, vegetation dynamics, structure and climate (Faegri and Iversen, 1989). Over-representation of pollen types occurs because pollen is produced abundantly or disperses easily; wind-pollinated plants are typically better represented in pollen rain than animal-pollinated species (Jacobson and Bradshaw, 1981). Therefore, pollen representation is often related to the pollination mode (e.g. wind, animals) (e.g. Fletcher and Thomas, 2007; de Nascimento et al., 2015). Little work has been carried out on the pollen vectors of Australian plant taxa, with the existing literature revealing a large variety of biotic mechanisms controlling the pollination of Australia's flora (e.g. Armstrong, 1979; Serventy and Raymond, 1974; Paton and Ford, 1977; Ford et al., 1979; Hopper, 1979; Hopper and Moran, 1981; Irvine and Armstrong, 1990). The pollination behaviour of the most studied plant taxa in Australia remains uncertain: for instance, *Eucalyptus* (Australia's most common canopy dominant) is mostly commonly believed to be a zoophilous plant taxon pollinated by birds, mammals and insects (Armstrong, 1979; Regal, 1982), but anemophily has been suggested to occur in a few species (Pryor, 1976). Furthermore, while zoophily has also been suggested for many other sclerophyllous taxa in this region (e.g. Proteaceae and Myrtaceae) (Regal, 1982), no information is available for the key components of much of the Australian flora including the temperate rainforests that occupy the wettest parts of Australia's southeast.

Implicitly or explicitly, all interpretations of pollen diagrams make assumptions about pollen dispersal and source area. These parameters have been modelled in various ways (Prentice, 1985; Sugita, 1993, 1994; Kuparinen et al., 2007; Theuerkauf et al., 2013), with the Gaussian Plume Model underpinning the LRA (Prentice, 1985; Sugita, 1993, 1994) being the most widely-used model of pollen dispersal. The GPM is based on Sutton's air pollutant plume dispersion equation (Sutton, 1953). The model has been calibrated using the concentration of particles (e.g. pollen) several hundred meters downwind from a point source as spreading outward from the centreline of the plume following a normal probability distribution. The GPM fails to realistically predict particle dispersal over longer distances, which is largely governed by vertical airflows and updrafts (Kuparinen et al., 2007). Fully mechanistic dispersal models such as the Lagrangian Stochastic Model (LSM) describe pollen dispersal more realistically and may be therefore more suitable to model pollen deposition in lakes (Theuerkauf et al., 2013). In contrast to the Gaussian Plume Model, when considering pollen spectra from lake surface sediments, the Lagrangian Stochastic Model gives greater importance to pollen arriving from 10 to 100 km distance (Theuerkauf et al., 2013).

Pollen dispersal models are used to estimate two key parameters of the quantitative vegetation reconstruction algorithm: Pollen Productivity Estimates (PPEs) and Relevant Source Area of Pollen (RSAP). PPEs are a measure of the amount of pollen released for transport per unit area of pollen-producing vegetation (grains/m²/yr). PPEs are derived from surface sample studies and usually expressed as a dimensionless ratio relative to a reference taxon (Relative Pollen Productivity) (Bunting et al., 2013). Notwithstanding the assumed pollination mechanisms adopted by plant taxa, pollen productivity may be effectively estimated using a dataset of modern pollen and distance-weighted vegetation abundance (e.g. Broström et al., 2008). The RSAP is defined by a radial distance from a sampling point, beyond which the relationship between pollen and cumulative distance-weighted vegetation data does not improve (Sugita, 1994). The RSAP is affected by a

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