



## Research paper

## Pollen–vegetation relationships at a tropical cloud forest's upper limit and accuracy of vegetation inference

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## ABSTRACT

Palaeoecological records are increasingly needed from tropical montane systems. To infer past tropical vegetation dynamics, understanding modern pollen–vegetation relationships is required, but understanding effects of different sampling media between calibration datasets and palaeorecords is also needed. This is especially true when palaeorecords are derived from bogs or lakes with boggy shores and common wetland plants share the same pollen taxon with important upland plants that distinguish tropical vegetation types (e.g., Poaceae and *Plantago*). We assessed modern pollen–vegetation relationships around an upper cloud forest line in the Hawaiian Islands and tested the utility of a modern pollen calibration dataset derived from 88 surface soil samples when applied in 10 test wetland sites more typical of palaeorecords. We assessed over- and under-representation of pollen/spore taxa with a direct comparison to plant abundance and derived several metrics from the pollen/spore assemblages – analogs, ordinations, relative abundance of life forms, and ratios of life forms. We used the Receiver Operator Characteristic (ROC) to (1) compare metric performance at distinguishing vegetation around the upper forest line, (2) assess whether excluding wetland taxa significantly affected metric performance, and (3) test the accuracy of vegetation inference. Pollen–vegetation relationships were influenced by great ecological breadth and over- or under-representation of pollen and spores, which could be explained by pollination syndrome (wind vs. animal), grain/spore mass and upslope transport in winds. However, we found no evidence that upslope transport significantly blurred the upper-forest-line signal here, likely because winds are predominantly perpendicular to slope, and vertically constrained by the trade-wind inversion. Pollen from Poaceae and *Plantago* characterizes vegetation around this Hawaiian upper forest line and dominates wetland assemblages. Removing wetland taxa from the modern pollen calibration dataset levied no cost on a metric's performance, and greatly reduced the incidence of inaccurate vegetation inference in test sites. Minor error rates remained when rare, over-represented, or ecologically broad types were used in isolation. Overall, this study demonstrates that inferring forest line position from fossil pollen/spore assemblages requires careful consideration because (1) differences in sampling media between the modern calibration dataset and palaeorecords create opportunity for inaccurate vegetation inference and (2) some metrics perform better than others.

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## 1. Introduction

High elevations are projected to warm faster than low elevations across the globe, particularly in the tropics (Bradley et al., 2004; Thompson et al., 2011). Recent trends show that tropical montane regions are indeed warming rapidly – 0.34 °C/decade across the tropical Andes (Vuille and Bradley, 2000) and 0.27 °C/decade in the Hawaiian Islands at the northern limit of the Tropics (Giambelluca et al., 2008; Juvik et al., 2011). The advent of rapid climate change in tropical montane ecosystems raises great concern because these ecosystems supply water, store carbon, and support high levels of biodiversity and,

particularly in island ecosystems, endemism (Loope and Giambelluca, 1998; Foster, 2001; Buytaert et al., 2011). Understanding the climate-change sensitivity of these tropical mountain ecosystems is needed (Loope and Giambelluca, 1998). Vegetation's sensitivity to climate is well documented in fossil pollen records, which can be used to inform conservation planning (e.g., Davis et al., 2000; Bush, 2002a; Gilson and Willis, 2004; Gosling and Bunting, 2008), particularly when they are calibrated with a modern pollen dataset. In the tropics, numerous studies show that modern pollen rain distinguishes vegetation types (Reese and Liu, 2005; Bhattacharya et al., 2010; Burn et al., 2010; Collins and Bush, 2010), and reflects altitudinal gradients in plant community composition and some individual plant taxa (Weng et al., 2004; Kennedy et al., 2005; Rull, 2006; Olivera et al., 2009; Correa-Metrio et al., 2011; Urrego et al., 2011). With this strong elevational signal, pollen rain can detect the turnover in vegetation at

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the lowest reaches of cloud forest (Weng et al., 2004; Urrego et al., 2011) and at the upper forest line (Weng et al., 2004; Rull, 2006; Olivera et al., 2009; Niemann et al., 2010), both of which are expected to be sensitive to climate change.

We generally expect a relationship between modern pollen rain and vegetation; but that relationship is not straightforward, particularly in montane systems. Under- or over-representation of pollen and spores has long been identified as an important problem in pollen analysis and can largely be explained by various differences in pollination syndrome – wind or animal (Hansen, 1949; Markgraf et al., 1981; Niemann et al., 2010). Pollen rain along montane gradients is particularly susceptible to upslope and extralocal transport of pollen and spores in the wind (Markgraf, 1980; Bush, 2000; Di Pasquale et al., 2008; Collins and Bush, 2010; Niemann et al., 2010). Upslope transport leads to overrepresentation of arboreal pollen taxa above the upper forest line, and therefore potentially complicates reconstructions of upper forest line dynamics (Weng et al., 2004; Olivera et al., 2009; Niemann et al., 2010). Understanding the modern pollen–vegetation relationship is an important first step for reconstructing past dynamics in tropical montane vegetation.

A second problem in tropical pollen analysis occurs because the sampling media of calibration datasets often differs from that of palaeorecords. Modern pollen calibration datasets in the tropics are typically derived from upland surface soil samples, moss polsters, or pollen traps, because few lakes and bogs are available to build a robust calibration dataset from the same depositional environment as palaeorecords (but see Rull, 2006). The different sampling media are broadly similar (Olivera et al., 2009; Burn et al., 2010; Lisitsyna et al., 2012), but each can experience different taphonomic effects, represent different temporal and spatial scales, and have different biases toward over- or under-representation. Over-representation of wetland taxa in palaeorecords collected from bogs or lakes with boggy shores is a particularly challenging aspect of using a modern pollen calibration dataset derived from a different medium to infer past vegetation. Plants occupying wetlands surrounding the palaeorecord site will be over-represented in pollen/spore assemblages derived from these wetland sediments, regardless of the surrounding upland vegetation (e.g., Bush, 2002b; Gosling et al., 2009). Often these wetland plants are members of Asteraceae, Poaceae, and *Plantago*, and unfortunately, these same pollen taxa are also important for distinguishing tropical vegetation types such as forested versus non-forested tropical lowlands (Bhattacharya et al., 2010), cerrado versus rainforest (Gosling et al., 2009), páramo versus cloud forest (Weng et al., 2004; Olivera et al., 2009), or the puna grassland of the Altiplano versus other vegetation types (Reese and Liu, 2005). This is an important problem. It has strong implications for the accuracy of palaeoecological reconstructions, particularly near upper forest lines, but it has received little attention. Understanding differences between pollen assemblages recovered from different media – surface soils, moss polsters, pollen traps, and wetland sediments – is a crucial second step to providing accurate reconstructions of past tropical montane vegetation dynamics that inform conservation planning.

In addition, several techniques have historically been used to reconstruct vegetation from pollen assemblages and some may be better than others. Ordinations and the modern analog technique (based on similarity or dissimilarity measures) have a long history in pollen-based vegetation inference (Prentice, 1980; Overpeck et al., 1985; Williams and Shuman, 2008). Ratios of important pollen taxa have also proven useful to distinguish among vegetation types, particularly when overall pollen percentages do not differ dramatically between vegetation types (Maher, 1963; Lynch, 1996; Calcote, 1998; Herzsuh, 2007; Hotchkiss et al., 2007). Vegetation around tropical upper forest lines has been distinguished with percent arboreal pollen (Olivera et al., 2009; Niemann et al., 2010) and can clearly be seen in the primary axis of ordinations (Weng et al., 2004; Rull, 2006). Which of these metrics derived from a modern pollen calibration

dataset is best for reconstructing a tropical montane upper forest line? How does excluding wetland pollen taxa – including types like Poaceae that are also important on the upland landscape – influence the discrimination power of each metric? And finally, how accurate is vegetation inference in palaeorecords derived from wetland sediments, when the modern pollen calibration dataset is derived from surface soils?

We assessed modern pollen–vegetation relationships around an upper cloud forest line in the Hawaiian Islands and tested the utility of a modern pollen calibration dataset derived from surface soils, in wetland settings. We analyzed modern pollen/spore assemblages from 88 upland surface soil samples collected in vegetation plots, and assessed over- and under-representation of pollen/spore taxa with a direct comparison to plant abundance. We used the Receiver Operator Characteristic (ROC, e.g., Metz, 1978; Gavin et al., 2003) to compare how different pollen-based metrics – analogs, ordinations, relative abundance of life forms, ratios of life forms – distinguish the cloud forest from the subalpine–alpine vegetation above the cloud forest's upper limit. We also used ROC to assess whether excluding wetland taxa from pollen and spore assemblages significantly affected a metric's ability to distinguish vegetation types around the upper forest line. Finally, we tested the accuracy of vegetation inference when a modern pollen calibration dataset, based upon surface soils, was used in wetland sediments.

## 2. Study area

### 2.1. Physical setting

The main Hawaiian Islands are situated a few degrees below the Tropic of Cancer and are near the poleward edge of the Hadley Cell (Fig. 1a). As a result of this geography, high elevations in the Hawaiian Islands are under the influence of the trade-wind inversion (TWI), a synoptic subsidence inversion which prevents orographic precipitation or cloud formation above its base height of ~2100 m. The TWI establishes a dramatic discontinuity of humidity and potential evapotranspiration (Giambelluca and Schroeder, 1998) which coincides with the upper limit of cloud forest (Kitayama and Mueller-Dombois, 1992; Leuschner, 2000; Crausbay and Hotchkiss, 2010). The summit of Haleakalā volcano (20°42'35" N, 156°15'12" W), on the island of Maui, Hawai'i rises above the TWI to 3055 m and the study area is situated between 1900 m and 2400 m elevation on the windward northeast slope (Fig. 1b). The study area brackets the elevation of the mean TWI (~2100 m) and the cloud forest's upper limit (Fig. 1b). It also encompasses a strong easterly, cross-slope rainfall gradient which follows the average direction of the northeasterly trade winds and amounts to ~500 mm km<sup>-1</sup> year<sup>-1</sup>, such that the eastern forest line in the study area receives more rainfall (~5000 mm year<sup>-1</sup>) than the western forest line (~3500 mm year<sup>-1</sup>, Crausbay and Hotchkiss, 2010). The study area includes 134 vegetation plots including the upper ~300 m of cloud forest and the subalpine shrubland and alpine grassland-scrubland ecosystems ~300 m above the forest line. In addition, the study area includes 10 test bog and lake sites forming an elevational gradient along the northeast volcanic rift zone of Haleakalā volcano (Fig. 1b).

Haleakalā volcano is in its post–shield building stage and the soils are derived from several basaltic rock types: 'a'ā (rough) and pāhoehoe (smooth) lava flows and associated cinder and spatter, vent deposits, and ash falls (Sherrod et al., 2007). Several bogs and two small lakes occur along Haleakalā's wettest area, in the northeast volcanic rift zone, from 1450 to 2300 m elevation (Fig. 1b). These wetland systems develop in flat, low-lying areas at the base of cinder cones, within collapsed cinder cones, or at the summits of eroded secondary cones, and are associated with a deeper, water-impervious placic horizon (Loope et al., 1991). Most of these wetland systems occur below the TWI in the cloud forest, but one bog exists above

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