Montane bias in lowland Amazonian peatlands: Plant assembly on heterogeneous landscapes and potential significance to palynological inference

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ABSTRACT

Past temperature changes in tropical mountain regions are commonly inferred from vertical elevational shifts of montane indicator taxa in the palynological record. However temperature is one of several abiotic factors driving the low-elevational limits of species and many montane taxa can occur in warmer lowlands by tracking appropriate habitat types, especially highly flooded wetlands. In this paper we explore ways in which lowland habitat heterogeneity might introduce error into paleo-temperature reconstructions, based on field data of seven modern peatland vegetation communities in the southern Peruvian Amazon (~200 masl). Peat-rich substrates are common edaphic transitions in pollen cores and provide detailed records of past vegetation change.

The data show that indicators of modern peatlands include genera with montane as well as lowland distributions, while indicators of surrounding forests on mineral substrates have predominantly lowland distributions. Based on family-level analyses we find that modern peatland vegetation communities have taxonomic compositions appearing to be 389 m to 1557 m (mean = 1050 ± 391 m) above their actual elevations due to a high abundance and number of families with high elevation optima.

We interpret the relatively higher prevalence of montane elements in modern peatlands as habitat tracking of a conserved montane niche on heterogeneous lowland landscapes. We suggest that both high moisture availability and stressful edaphic conditions of peatland habitat may explain the montane bias observed. To the extent that fossilization provides a better record of past vegetation that occurred proximate to the site of deposition, we suggest that habitat tracking of montane elements may introduce a cool bias in lowland paleo-temperature reconstructions based on pollen proxies.

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1. Introduction

Climatic interpretation of fossil pollen assemblages along elevational gradients plays a prominent role in our understanding of neotropical climate change, especially in paleo-temperature reconstruction (Farrera et al., 1999; Weng et al., 2004). Many taxa tend to reach their highest diversity and abundance along a limited elevational range as they track appropriate conditions along mountain slopes. Terrestrial pollen records document the vertical migration of stenothermic taxa in response to past climate change, so knowledge of adiabatic lapse rates can be used to convert elevational shifts to temperature change. This method is standard practice and has been especially important in quantifying past temperature depression from the down slope migration of neotropical montane elements during Pleistocene glacial periods (Bush et al., 1990; Colinvaux et al., 1996; Groot et al, 2011).

The contemporary distribution patterns of higher-level taxa (e.g., families and genera) along mountain slopes are expected to be the result of niche differences across space, however we know little about specific ecological factors underlying these distribution patterns (Körner, 2007; Wiens, 2011). While temperature is often assumed to play a prominent role, this single variable is likely only one of a variety of abiotic and biotic factors expected to drive the lower elevational range limits of montane taxa (Bush et al., 2004; Grubb, 1971; Körner, 2007; Wiens, 2011). For example, on modern landscapes a number of montane indicator taxa with characteristic peaks in diversity and abundance in high elevation regions are also represented in nearby Amazonian lowlands by one to few species, including *Hedyosmum* (Chloranthaceae), *Panopsis* (Proteaceae), *Podocarpus* (Podocarpaceae),

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Salix (Salicaceae), *Ternstroemia* (Pentaphylaceae), *Ilex* (Aquifoliaceae), and others (Colinvaux et al., 2000; Marchant et al., 2002; Van der Hammen and Hooghiemstra, 2000). While these montane taxa are exceedingly rare in most lowland forest types, they can become abundant in stressful edaphic conditions, and especially in highly flooded wetland habitats (Gentry, 1982; Marchant et al., 2002; Oliveira-Filho and Ratter, 1995; Steyermark, 1979). Apparent tracking of many montane elements to particular lowland habitats suggests that the abiotic and biotic conditions in which they can successfully disperse and regenerate on lowland landscapes may be constrained by a highly conserved niche (Ackerly, 2004; Harrison and Grace, 2007; Pillon et al., 2010; Wiens, 2011; Wiens and Donoghue, 2004; Wiens et. al., 2010).

The ecological and evolutionary processes that determine how montane elements are assembled on modern heterogeneous lowland landscapes may be relevant to palynological inference, and especially paleo-temperature inference, in at least two ways. First, the quality of paleo-temperature interpretation is dependent upon an adequate understanding of the drivers of species low-elevational range limits, which are often poorly known (Körner, 2007). To the extent that montane elements tend to occupy lowland sites that are most suitable to their conserved phenotypes (Ackerly, 2004; Wiens, 2011), increased understanding of the ecological conditions in which they occur in the lowlands can reveal insight into factors — other than temperature — that might influence distribution patterns of montane elements through time. Second, habitat tracking of an ancestral niche on heterogeneous lowland landscapes can strongly alter the taxonomic composition and biogeographic signatures of local vegetation communities during community assembly, independent of regional climate change (Kubitzki, 1989; Prance, 1979; Pyke et al., 2001; Wittmann et al., 2013). Because

vegetation directly occupying fluvial or depositional sites (i.e., wetland vegetation) is known to contribute disproportionately to pollen sums, the ecological sorting processes operating at local scales have the potential to influence the biogeographic signature of fossil assemblages and, in turn, the climate interpretations made from them (Berrio et al., 2002; Burnham et al. 2001; Marchant et al, 2009). Indeed, in some cases, alternative interpretations of past climate change seem to have been fueled by disagreement in the importance of climatic versus local ecological processes in explaining compositional shifts in fossil pollen assemblages through time (Colinvaux et al., 2000; Punyasena et al, 2011; Van der Hammen and Hooghiemstra, 2000).

In this study we develop a biogeographic framework to examine the modern taxonomic composition of peatland habitat in the southern Peruvian Amazon. Peat-rich substrates are commonplace in pollen records and have provided detailed accounts of past vegetation (e.g. Colinvaux et al., 1996; Liu and Colinvaux, 1985; Roucoux et. al. 2013). Making use of a publically available network of woody vegetation inventories established across a wide elevational gradient we examine the degree to which the taxonomic compositions of woody peatland communities reflect that which would be expected given their actual elevation.

2. Methods

2.1. Study region

The peatland system considered in this paper is located within the subsiding Beni-Mamore foreland basin below 250 masl in the Department of Madre de Dios in the Amazon region of southern Peru (Fig. 1). The main drainage tributary is the Madre de Dios River, an actively
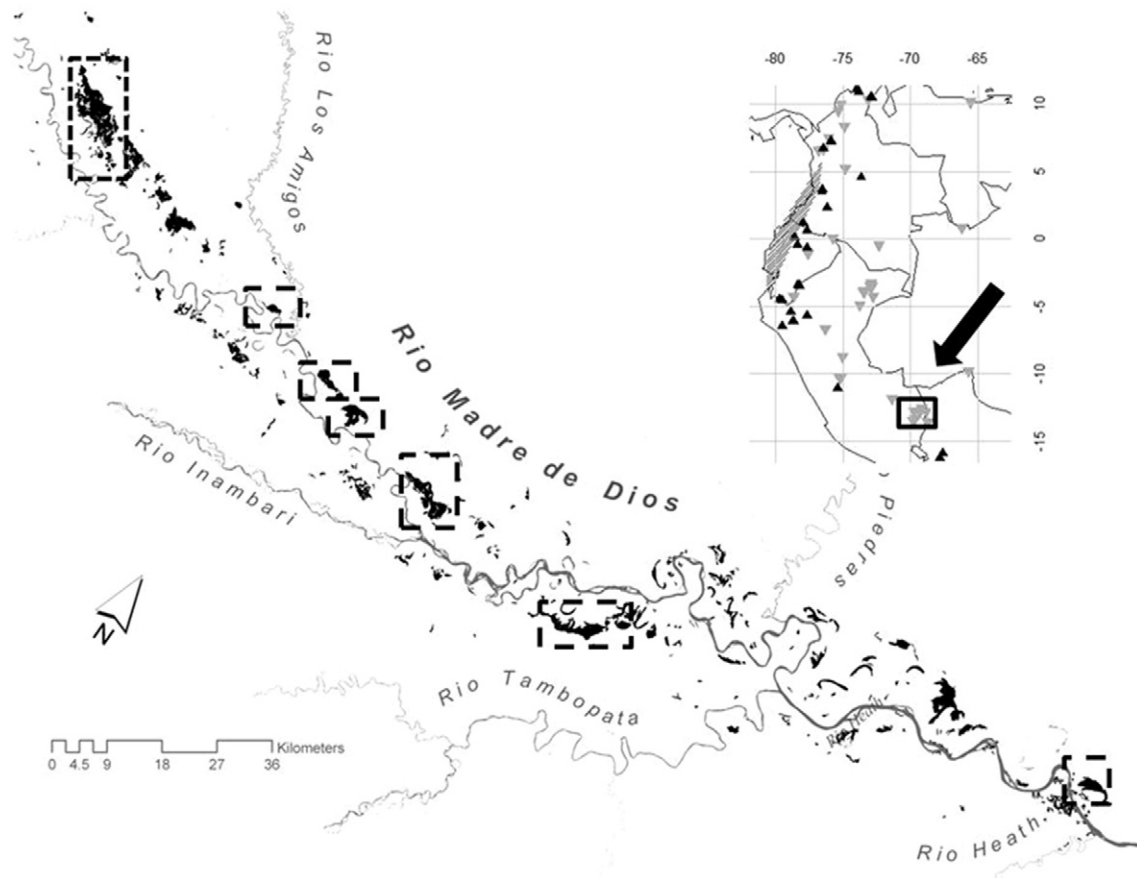

Fig. 1. The 250-km stretch of the main drainage tributary of the southern Peruvian Amazon where focal peatlands (black) are located. Inventoried peatlands are outlined. Peatland names (from west to east; Table 3) are COLO, CICRA, HUIT 1, HUIT2, LAGA, MERC, and BOLI. The inset map shows the location of the 76 plots obtained from the Gentry transect data in relation to the peatland study area. Black and gray triangles represent Gentry sites at elevations greater than and less than 1000 masl, respectively. The shaded area corresponds to the Chocó region included in the supporting analysis (see Section 4.1.1).