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Seasonality, montane beta diversity, and Eocene insects: Testing Janzen's dispersal hypothesis in an equable world

S. Bruce Archibald [a,b,c,*], David R. Greenwood [d,1], Rolf W. Mathewes [a,2]

[a] Dept. of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada
[b] Royal BC Museum, Victoria, BC, Canada V8W 1A1
[c] Museum of Comparative Zoology, Cambridge, MA, 02138, USA
[d] Biology Dept., Brandon University, Brandon, MB, R7A 6A9, Canada

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ABSTRACT

We test Janzen's (1967) hypothesis that the low temperature seasonality in the modern tropics accounts for increased local species turnover (beta diversity) across montane landscapes relative to those of the more seasonal Temperate Zone. In the Eocene, low seasonality extended beyond the hot tropics to Polar Regions, therefore, its effects on montane dispersal ability should have been decoupled from low latitude. We sampled fossil insect communities across the Okanagan Highlands: a thousand kilometer transect of temperate, low temperature seasonality, higher mid-latitude Eocene uplands of far-western North America. We find high species turnover, supporting a prime role of temperature fluctuation in controlling montane beta diversity. This high upper mid-latitude montane endemism is consistent with greater Eocene global biodiversity.

1. Introduction

Understanding the causes of turnover in local species composition across a landscape – beta diversity – remains a major challenge in community ecology. In his influential paper *Why mountain passes are higher in the tropics*, Janzen (1967) proposed that the same elevation difference between a valley bottom and a mountain pass would constitute a stronger physiological dispersal barrier and consequently promote greater beta diversity in the tropics compared to temperate latitudes. In the Temperate Zone, the wide difference between summer and winter temperatures would foster wider temperature tolerance, and also provide an overlap of temperatures between mountain passes and valley bottoms during part of the year. In the tropics, however, low temperature seasonality would foster adaptation to a narrower temperature range, and a valley bottom and mountain pass of the same elevation difference as in the Temperate Zone example would lack a common temperature over a year (Fig. 1). (Here, by seasonality, we refer specifically to temperature seasonality throughout.) An organism dispersing upslope at any time eventually would encounter a climate to which it was not adapted. Tropical highland climate would, therefore, promote increased beta diversity by virtue of stronger thermal dispersal barriers between valleys (intervening passes physiologically higher), between mountains (intervening lowlands physiologically lower), and along altitudinal gradients (mountains physiologically steeper). This would result in greater population fragmentation and isolation in tropical than in temperate mountainous regions. Such conditions would, hypothetically, foster allopatric speciation by cutting off gene flow between populations that, through episodic or singular dispersal, manage to cross such barriers (Cadena et al., 2012). Janzen's model has been supported by studies of a variety of organisms, including insects and vertebrate ectotherms and endotherms (Gaston and Chown, 1999; Ghalambor et al., 2006; Lewinsohn and Roslin, 2008; Jankowski et al., 2009; McCain, 2009; Calosi et al., 2010; Hazell et al., 2010).

The modern (but see Northern vs. Southern Hemisphere: Chown et al., 2004; Archibald et al., 2010) broad covariance of latitude, seasonality and mean annual temperature (MAT) has traditionally hampered isolation and assessment of their individual effects on large-scale diversity patterns. Studies using the fossil record, however, can in some cases circumvent such issues, allowing fresh views by exploiting the differing relationships between potential forcing factors in the past (Erwin, 2009; Archibald et al., 2010). Taking this perspective affords not only characterization of the history of large-scale diversity patterns, but also assessment of the impact of individual factors governing diversity patterns independent of time.

Paleontological studies of terrestrial beta diversity have generally focused on lowlands (Vavrek and Larson, 2010; Rose et al., 2011), or at the inter-province level (Van Valkenburgh and Janis, 1993). Others

* Corresponding author at: Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A 1S6. Tel.: +1 778 782-4458.
E-mail addresses: sba48@sfu.ca (S.B. Archibald), GreenwoodD@brandonu.ca (D.R. Greenwood), mathewes@sfu.ca (R.W. Mathewes).
[1] Tel.: +1 204 571 8543.
[2] Tel.: +1 778 782 4472.

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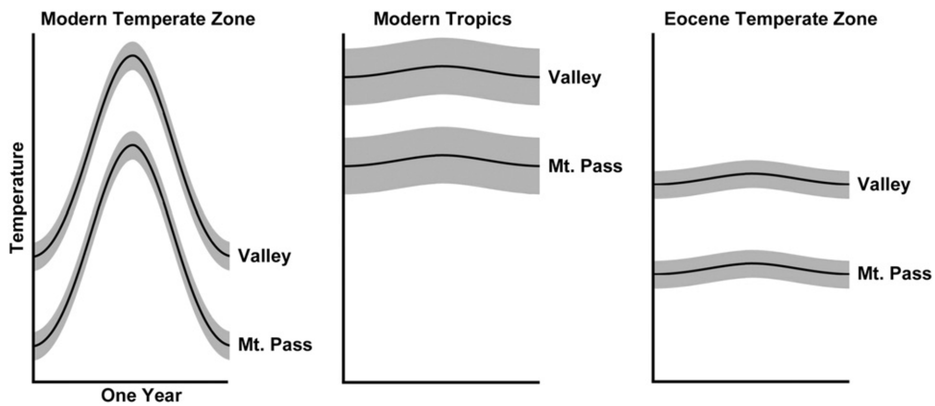

Fig. 1. Janzen's hypothesis, see text for explanation: yearly temperature variation in the Temperate Zone, the tropics, and as hypothesized for the Okanagan Highlands. Black lines are the mean temperature values over a year; gray indicates daily fluctuations.

have examined MAT and precipitation as explanatory climatic factors, with some debate on any effect of climate at all (Alroy et al., 2000; Woodburne et al., 2009). Topographic relief has also been tested for effects on alpha diversity and speciation (Gunnell and Bartels, 2001; Badgley, 2010; Finarelli and Badgley, 2010). Here, we explicitly test the central element of Janzen's hypothesis – temperature seasonality – in governing montane beta diversity by decoupling it from latitude through examination of communities in the context of the early Eocene global climatic regime.

In the early Eocene, low temperature seasonality was not restricted to the tropics, but extended into the High Arctic (e.g., Greenwood and Wing, 1995; Eberle and Greenwood, 2012; and see below). We took advantage of this fact by sampling fossil insects at localities in the early Eocene Okanagan Highland deposits of western Canada and the northwestern United States (Fig. 2). This area has a rich, well preserved insect fauna (Fig. 3) deposited in regional basins of considerable paleoelevation scattered across a roughly thousand kilometer transect (Greenwood et al., 2005; Archibald et al., 2011a). Okanagan Highland climate was mesic (annual precipitation > 100 cm/year), with upper microthermal to lower mesothermal MAT (~10–15 °C) as indicated by paleobotanical proxies, through both taxon dependent (bioclimatic) and taxon independent (leaf physiognomy) analyses (Greenwood et al., 2005; Smith et al., 2009, 2012). Sampled localities span an interval of about three and a half million years (2–4.8 Ma

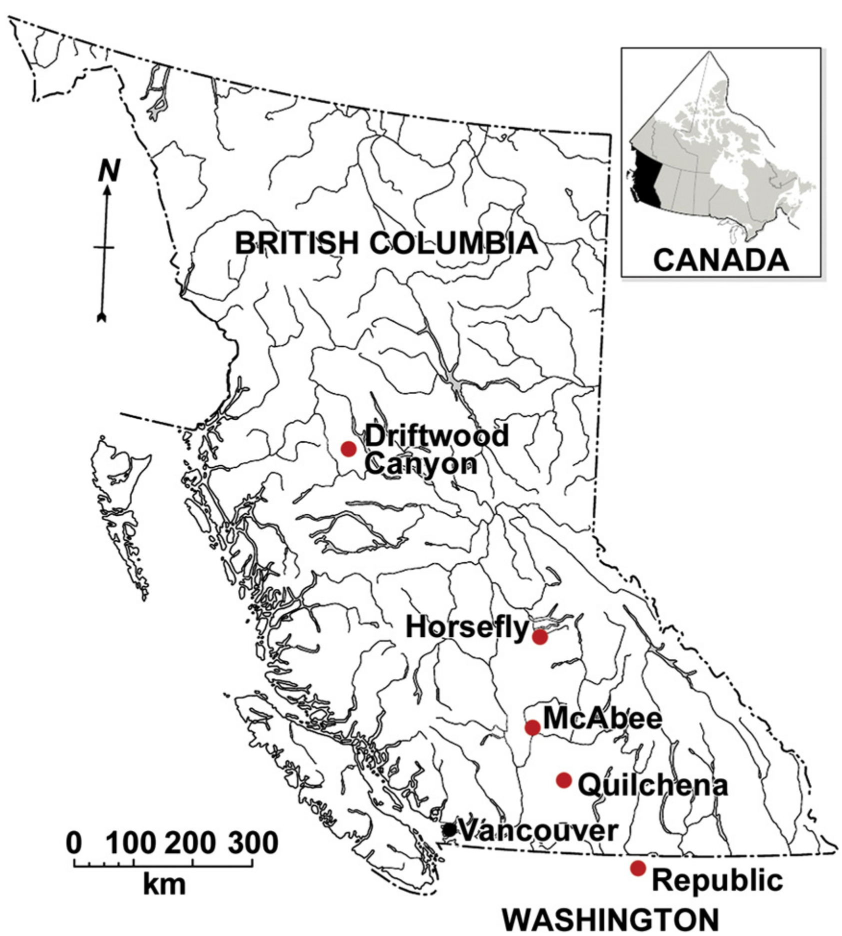

Fig. 2. Okanagan Highlands locations sampled (see text), and the city of Vancouver. Adapted with the permission of Natural Resources Canada 2013, courtesy of the Atlas of Canada. http://atlas.nrcan.gc.ca/site/english/maps/reference/outlineprov_terr/bc_outline.