



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

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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.

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### 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.

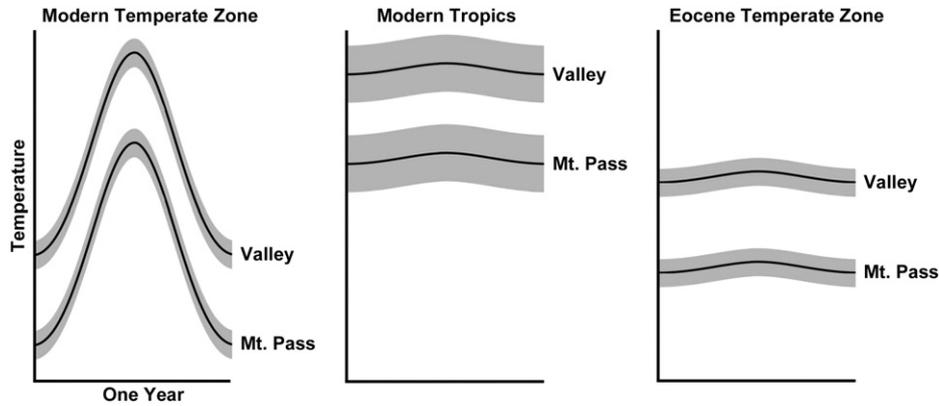
Paleontological studies of terrestrial beta diversity have generally focused on lowlands (Vavrek and Larson, 2010; Rose et al., 2011), or at the inter-province level (Van Valkenburgh and Janis, 1993). Others

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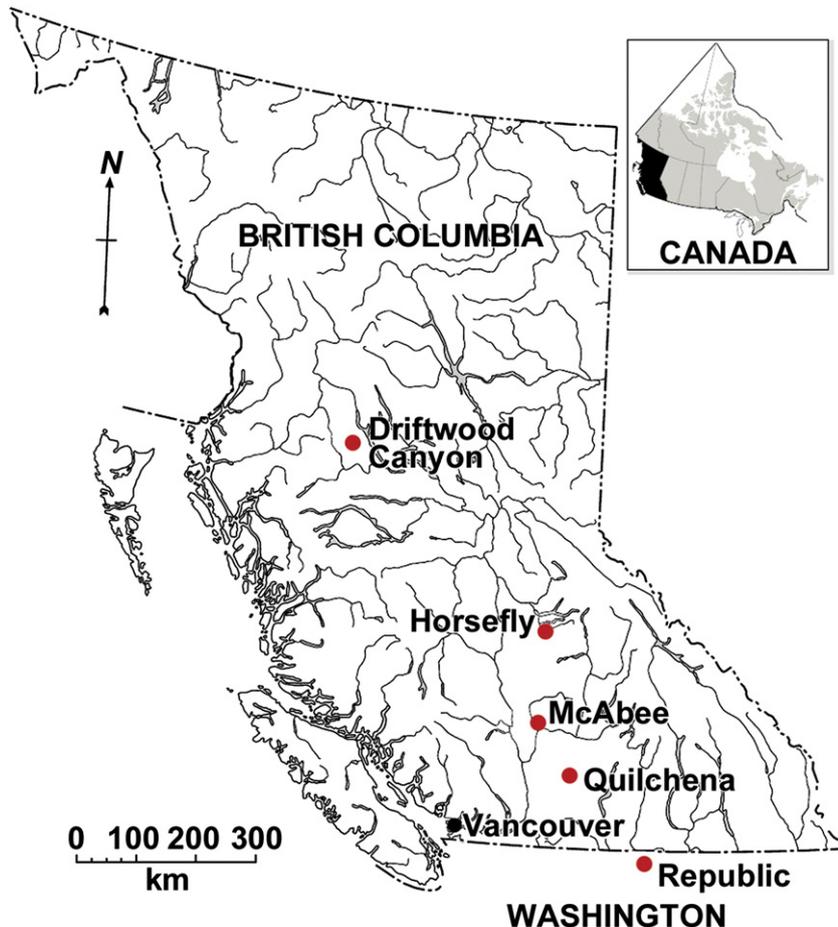


**Fig. 1.** Janzen's hypothesis, see text for explanation: yearly temperature variation in the Temperate Zone, the tropics, and as hypothesized for the Okanagan Highlands. Black lines are the mean temperature values over a year; gray indicates daily fluctuations.

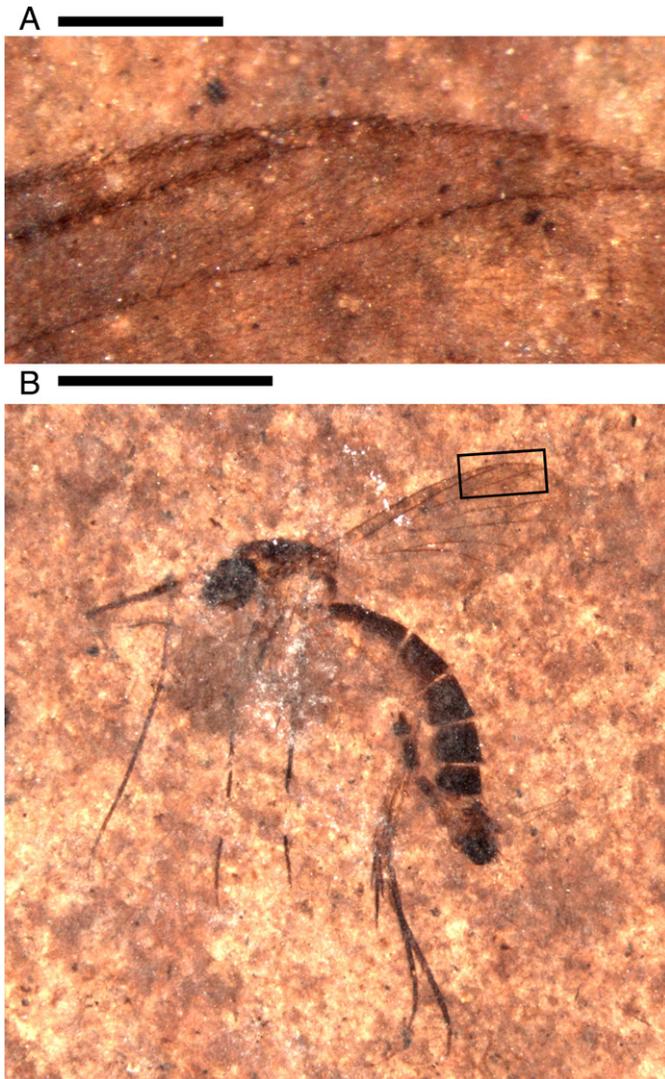
have examined MAT and precipitation as explanatory climatic factors, with some debate on any effect of climate at all (Alroy et al., 2000; Woodburne et al., 2009). Topographic relief has also been tested for effects on alpha diversity and speciation (Gunnell and Bartels, 2001; Badgley, 2010; Finarelli 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](http://atlas.nrcan.gc.ca/site/english/maps/reference/outlineprov_terr/bc_outline).



**Fig. 3.** Fine-level preservation of a fungus gnat from Driftwood Canyon, (A) complete insect; (B), close-up of the apical portion of the wing indicated by the box in (A), showing minute hairs (microtrichia) on the wing membrane. Scale bars: (A), 200  $\mu$ m; (B), 2 mm.

with error values) (Archibald et al., 2010, 2011a), and about 6° of latitude, slightly more northward than by tectonic movement.

Janzen's hypothesis is not dependant on latitude; it is only identified with it under modern conditions. It predicts that a mountainous transect with low temperature seasonality combined with the inherent elevational MAT gradient (see below) will necessarily generate high beta diversity. Finding low beta diversity in the higher mid-latitude montane Okanagan Highlands – where both low seasonality and an elevational MAT gradient are indicated – would, therefore, provide strong evidence that he was incorrect, and that some other, unknown factor explains observed high beta diversity across modern tropical montane regions.

### 1.1. Topography and elevational MAT gradient

Regional Paleogene uplift and associated volcanism reached peak activity in Okanagan Highland times, with lakes forming in grabens that filled with fossiliferous sediments. Topography consisted of mountains of high relief comparable to the modern British Columbian Coast and Selkirk ranges, drained by streams of steep gradients, interspersed with highland plateaus, and cut by deeply incised fluvio-lacustrine waterways (Ewing, 1980; Tribe, 2005). Coeval floras indicate a considerably warmer climate in nearby coastal lowlands,

and so a substantial elevational MAT gradient upslope to the Okanagan Highlands (Rouse et al., 1971; Mustoe and Ganaway, 1997; Wolfe et al., 1998; Greenwood et al., 2005; Smith et al., 2009).

Elevational temperature gradients are a function of the moist adiabatic lapse rate, which results from atmospheric properties such as moisture content and pressure that are independent of geological time. This has been widely applied in generating paleoaltitude estimates (e.g., Wolfe et al., 1998, Smith et al., 2009 for Okanagan Highland localities; and see reviews by Meyer, 1992, 2007).

### 1.2. Seasonality

A broad range of geochemical and biotic evidence indicates globally low temperature seasonality in the Eocene (Daley, 1972; Wing and Greenwood, 1993; Basinger et al., 1994; Greenwood and Wing, 1995; Archibald and Farrell, 2003; Shellito and Sloan, 2006a,b; Eldrett et al., 2009; Huber and Caballero, 2011; Eberle and Greenwood, 2012). Middle and high latitude Eocene communities are noted for their mixture of tropical and temperate-associated animals and plants, presenting a climatological problem that Daley (1972) explained by increased winter temperatures in regions of temperate MAT. Warming of winters by decreased temperature seasonality would allow frost-intolerant organisms to exist well outside their modern high MAT, low-latitude ranges into cooler latitudes and altitudes (Daley, 1972; Wing, 1987; Greenwood and Wing, 1995; Archibald and Farrell, 2003).

Under the low thermal seasonality of the early Eocene, frost intolerant 'tropical' organisms such as palms and crocodylians extended their ranges into much higher latitudes than today – as far north as 85°N – in regions with MATs of ~10–15 °C, resulting in communities that include organisms that are today segregated in tropical and temperate climates and latitudes (Daley, 1972; Estes and Hutchinson, 1980; McKenna, 1980; Budantsev, 1992; Wing and Greenwood, 1993; Basinger et al., 1994; Greenwood and Wing, 1995; Archibald and Farrell, 2003; Jahren, 2007; Markwick, 2007; Eldrett et al., 2009; Sluijs et al., 2009; Huber and Caballero, 2011; Eberle and Greenwood, 2012).

A tropical/temperate mix has been noted in various Eocene insect communities for over a century and a half. The presence of ant genera today restricted to circumpolar regions (e.g., *Leptothorax*) together with others now found exclusively in the tropics (e.g., *Gesomyrmex*) has been known in northern European Baltic amber since the mid-nineteenth century (Archibald and Farrell, 2003). Such climatically improbable co-occurrences are now recognized in other localities, for example, tropical ants, wasps, termites and other insects in the temperate MAT (~13.2 °C: Sheldon et al., 2009) late Eocene Bembridge Marls (UK) (Archibald and Farrell, 2003).

This pattern is expressed throughout the Okanagan Highlands. In spite of temperate MAT values (Greenwood et al., 2005; Smith et al., 2009, 2012), insects that are now restricted to the tropics such as dipterine cockroaches coexisted there with others such as snakeflies (Raphidioptera) that are today characteristic of temperate regions (Archibald and Mathewes, 2000; Archibald and Farrell, 2003). The Okanagan Highland forests contained both temperate-climate associated plants such as spruce (*Picea*) and those that cannot withstand frost days (Erwin and Stockey, 1991; Wehr and Manchester, 1996; Hopkins and Johnson, 1997; Greenwood et al., 2005; Moss et al., 2005). It is highly improbable that these communities were all situated by chance at the climatic limits of their frost-intolerant members, i.e., the elevation of the frost line. For example, Tribe (2005) estimated that the Okanagan Highlands Princeton Chert (between Republic and Quilchena), where palm megafossils are the most common monocots (Erwin and Stockey, 1991), had a paleoelevation several hundred meters above McAbee. If Tribe's model is correct, the 5 °C coldest month mean temperature frost line below which palms cannot survive would have been considerably upslope of McAbee. This raises the coldest month mean temperature there while maintaining the estimated microthermal MAT, indicating an even further reduction in seasonality.

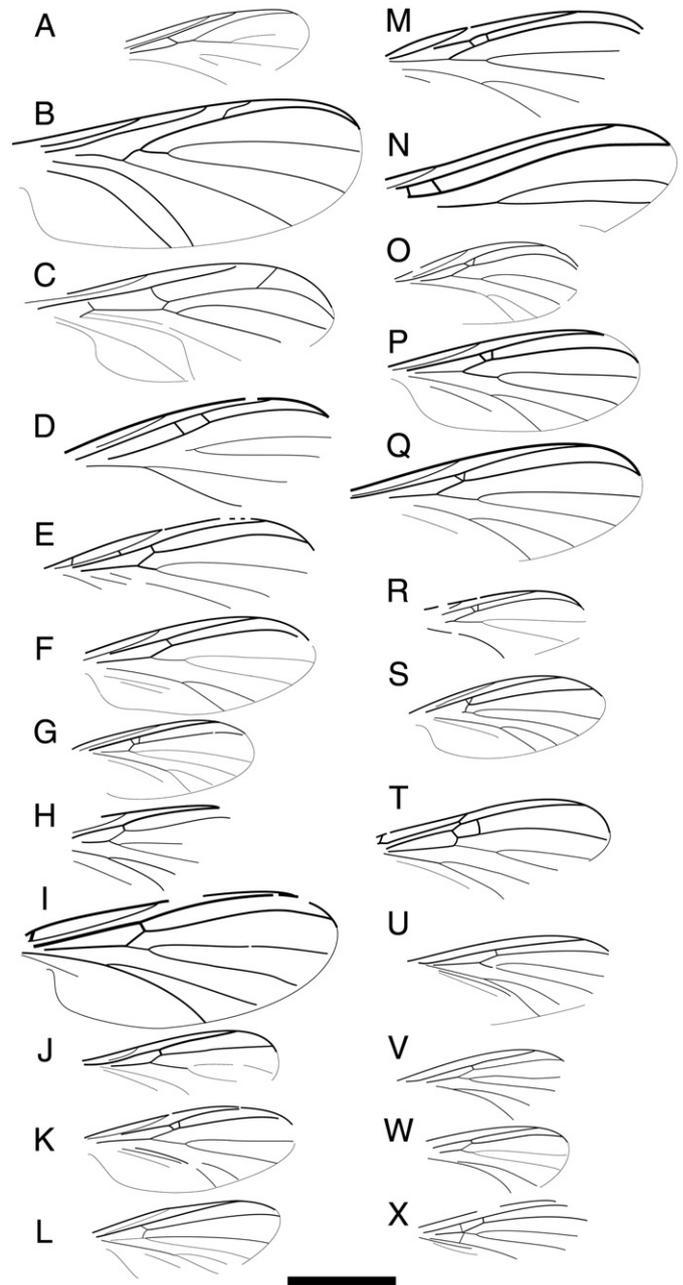
## 2. Materials and methods

Unbiased collections (all fossils identifiable as insect collected and data recorded) were made at McAbee (from the collection used by Archibald et al., 2010), Horsefly River, and Driftwood Canyon, British Columbia, Canada (coll. SBA); and at Republic, Washington, USA (coll. directed by SBA, see Acknowledgments). Museum collections were examined from McAbee (Thompson Rivers University, Kamloops, BC; Burke Museum, Seattle), Quilchena (coll. RWM) and Republic (coll. Stonerose Interpretive Center, Republic). Published occurrences were used for Ithonidae (Neuroptera) (including “Polystoechotidae”) (Archibald and Makarkin, 2006; Makarkin and Archibald, 2009) and Dinopanorpidae (Mecoptera) (Archibald, 2005). Specimens of five orders were evaluated, representing a variety of trophic guilds to control for host-limited dispersal (Table 1).

We expect a bias towards underestimating both alpha and beta diversities, as we emphasized species determinations by wing morphology (mostly forewings); some may have been divided further if examination of genitalia (for example) was possible. We followed a commonly used practice in modern large-scale insect surveys of separating specimens to morphospecies bins (Oliver and Beattie, 1993, 1996a,b). As in those studies, our goal was not to determine species identities (the names of orthotaxa), but rather to establish the (morpho)species present and compare these between sites. Samples of our species determinations are illustrated in Figs. 4 and 5 (Horsefly River Sciaroidea and McAbee Mecoptera, unnamed new family), and in the Supplementary online appendix (Fig. S1: Auchenorrhyncha from Republic and McAbee; Tipulidae from Driftwood Canyon, Horsefly River, Quilchena and Republic).

## 3. Results

We found between 468 and 470 species in 702 specimens examined (some similar auchenorrhynchs were placed in a few, small groups and treated as single species, see online Fig. S1) (Table 2). The rank abundance of specimens per species for each locality sample is illustrated in Fig. 6A–E. As can be seen in these plots, the majority of species at each site were represented by singletons, with few abundant species particularly showing (i.e., >10 specimens) at localities with larger sample sizes (McAbee, Republic). This reflects the well-documented insect community patterns found in the tropics (e.g., Price et al., 1995; see below), e.g., as recovered in a Costa Rican lowland rainforest (Fig. 6F). Beta diversity was high (Tables 3 and 4). Only four species were confidently shared between sites: the dinopanorpid scorpionfly *Dinokanaga dowsonae* (Republic, McAbee and Horsefly River); and three unnamed auchenorrhynch species (Horsefly River and Republic: 2; Quilchena and Republic: 1). Twelve instances were found of species



**Fig. 4.** Fungus gnat (Scaroidea) wings from Horsefly River, British Columbia, Canada: (A), Keroplatidae?; (B), Keroplatidae or Lygistorrhyninidae; (C), Bolitophilidae; (D–X), Mycetophilidae: (D), Leiinae; (E–K), Gnoristinae; (L–N), Gnoristinae or Sciophilinae; (O–S), Sciophilinae; (T), Mycomyiinae; (U–X), Mycetophilinae. (V) and (W) are assigned to the same species. Scale bar = 2 mm.

**Table 1**  
Insect taxa and trophic guilds sampled.

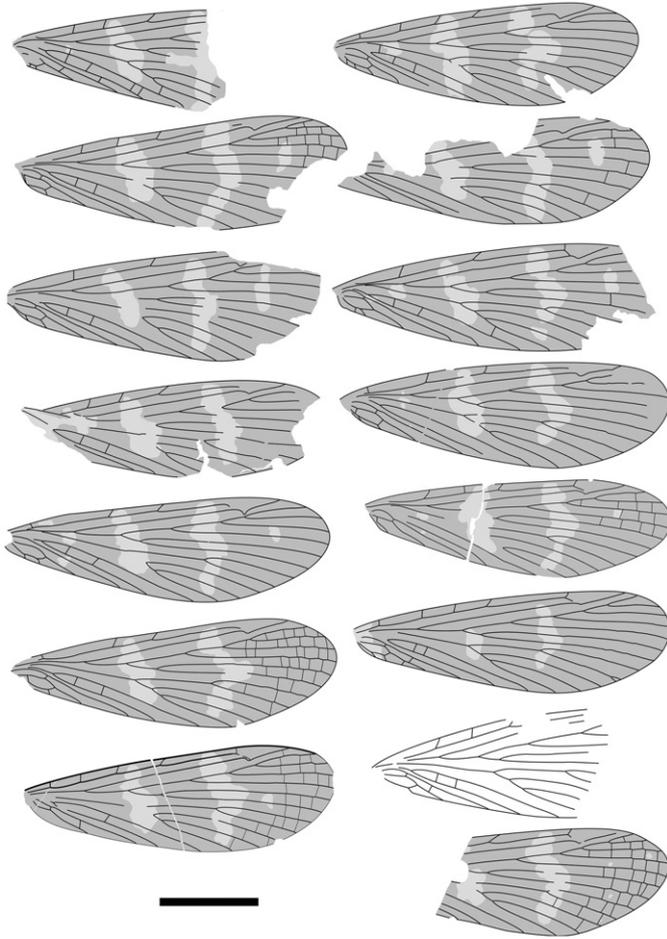
Taxon	Feeding	
Hymenoptera	Tenthredinidae	Herbivorous (leaf chewing); adults: pollen, nectar
	Ichneumonidae	Parasitoids
Diptera	Tipulidae	Saprophagous, phytophagous
	Empididae	Predaceous, some scavengers
	Syrphidae	Predaceous, saprophages; adults: pollen, nectar
	Sciaroidea	Fungivores, some predatory; adults: nectar, honeydew
Mecoptera	Dinopanorpidae	Carnivorous <sup>a</sup>
	unnamed family	Carnivorous <sup>a</sup>
Hemiptera	Auchenorrhyncha	Herbivorous (xylem, phloem feeders)
Neuroptera	Ithonidae	Little known

<sup>a</sup> Supposition that the two extinct Mecoptera families were carnivorous is supported by distinctive rostrum morphologies that match those of their living relatives who feed mostly by scavenging dead arthropods (Archibald and Mathewes current research).

possibly shared between sites: one of Auchenorrhyncha (McAbee and Republic); seven of tenthredinid sawflies (Horsefly River and McAbee: 2; Horsefly River and Republic: 1; Republic and McAbee: 4); two of the unnamed scorpionfly family (Republic and Quilchena: 1; Republic and McAbee: 1); one of empidid flies (Horsefly River and Driftwood Canyon); and one of fungus gnats (Horsefly River and Driftwood Canyon).

## 4. Discussion

Although the high level of insect alpha diversity recovered at these sites would be certainly surprising in the modern Temperate Zone, it is unremarkable in the modern tropics. While particular estimates of the total number of modern tropical insect species have been debated,



**Fig. 5.** Forewings of undescribed Mecoptera family specimens from McAbee, all assigned to the same species. Scale bar = 5 mm. Color patterning depicted where preserved (value, not hue).

it is well-established that it is extraordinarily high (“megadiversity”: Richardson and Arias-Bohart, 2011); indeed, the majority of species of multicellular life are thought to be tropical arthropods, mostly insects (Erwin, 1982; May, 1990; Gaston, 1991; Godfray, et al., 1999; Novotný and Basset, 2000; Lewinsohn and Roslin, 2008). Tropical insect diversity is characterized by many rare species, in a great number of studies represented by single specimens, even with large samples (above authors and Price et al., 1995; Novotný and Basset, 2000; Richardson and Arias-Bohart, 2011; and references in these). We recovered this same pattern of high richness with many rare species in the cooler, mid-latitude Okanagan Highlands, which, like the modern tropics, experienced low temperature seasonality (Fig. 6; and see detailed discussion by Archibald et al., 2010).

**Table 2**

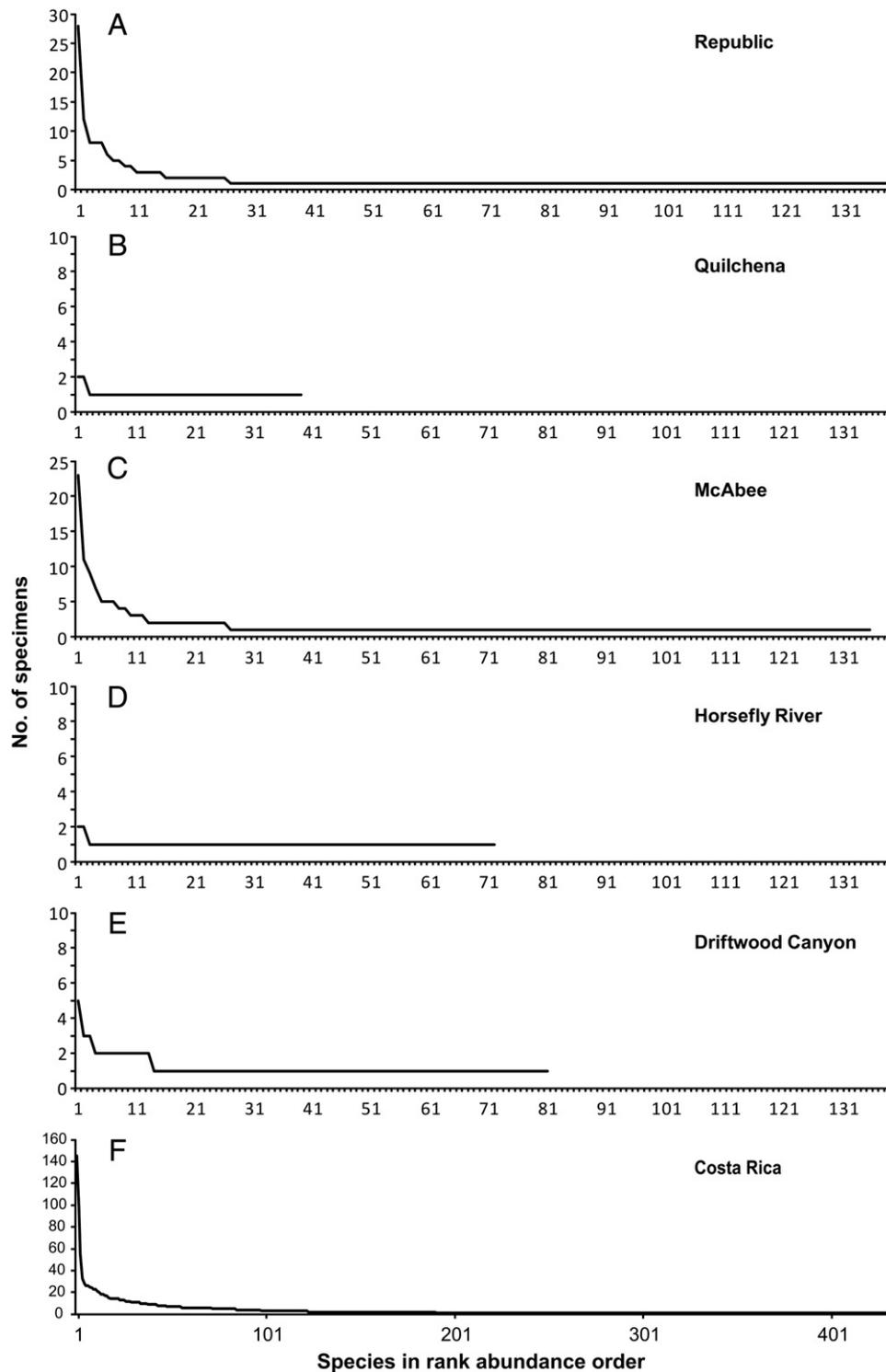
Insect taxa and quantities sampled by locality (number of species/number of specimens). Abbreviations: DC, Driftwood Canyon; HR, Horsefly River; Mc, McAbee; Qu, Quilchena; Re, Republic.

Taxon	DC	HR	Mc	Qu	Re	Total
Tenthredinidae	1/1	6/6	20/21	–	7/7	34/35
Ichneumonidae	35/44	7/7	34/48	11/11	7/7	94/117
Tipulidae	9/11	13/13	10/13	3/3	9/12	44/52
Sciaroidea	30/31	23/24	10/11	3/4	2/2	68/72
Empididae	3/5	7/7	–	–	2/2	12/14
Syrphidae	3/7	–	6/7	1/1	1/1	11/16
Dinopanorpidae	–	2/2	2/11	–	3/5	7/18
Unnamed family	–	–	1/23	1–2/2	3–4/6	5–7/31
Auchenorrhyncha	–	13/15	53/86	15/15	100/216	181/332
Ithonidae	–	1/1	–	4/5	7/9	12/15
Total	81/99	72/75	136/220	38–39/41	141–142/267	468–470/702

Contrary to traditional thought, it seems that low extra-tropical species diversity – not high tropical species diversity – is the anomalous phenomenon requiring explanation (Blackburn and Gaston, 1996), and that progress in understanding the modern latitudinal gradient of species diversity may be gained by examining the labile forcing factors now attenuating extra-tropical species diversity (Archibald et al., 2010). Multiple lines of evidence show that this pattern was established some time after the Eocene, when high levels of diversity extended far outside of the tropics into regions of temperate MAT. Insect diversity at the Okanagan Highland locality at McAbee is comparable with that of a Costa Rican Neotropical lowland rainforest (Archibald et al., 2010). This pattern was replicated in Okanagan Highland plants in various studies at McAbee, Falkland, and Republic (Wilf et al., 2003; Archibald et al., 2010; Smith et al., 2012). Tropical levels of plant diversity were also found in Paleocene Colorado (Johnson and Ellis, 2002) and Eocene mid-latitude Argentina (Wilf et al., 2003). High diversity of insect feeding damage types on Eocene leaves in Argentina supports complex, tropical levels of plant–insect interactions at least into mid-latitudes (Wilf et al., 2005). Mid-latitude North American marine molluscs also show high diversity (Addicott, 1970). Consistent with these findings, low or absent latitudinal gradients of species richness have been shown for Paleocene mammals (Rose et al., 2011) and various Eocene marine organisms (Taylor et al., 1980; Thomas and Gooday, 1996). This pattern extends into the Mesozoic, with dinosaur diversity levels peaking in mid-latitudes (Mannion et al., 2012). Those conditions diminishing modern extra-tropical diversity were, therefore, not operating until at least the end of the Eocene. This factor appears to be the later Cenozoic establishment of high seasonality outside of the tropics (Archibald et al., 2010).

Species originations, extinctions, and immigration within Okanagan Highland time are unlikely to have contributed more than a minor effect on our results. Insect species appear almost completely stable over the interval spanning the severe climatic disturbances and associated ecophysiological stress of the Ice Ages; out of over two thousand Quaternary beetle species examined in one study, only one or two are not known to exist today (Coope, 2004). Even as far back as the Eocene, eight insect species (including one from Driftwood Canyon) are known that are morphologically indistinguishable from modern species (Hörschemeyer et al., 2010). Major intercontinental dispersals of plants and mammals have been recognized across high latitude land bridges connecting North America with East Asia and Europe from the latest Paleocene through Okanagan Highland times (Archibald et al., 2011b); recently, this has been shown in insects, with some similarities to the genus level between the early Eocene of Europe and North America, including the Okanagan Highlands (reviewed by Archibald et al., 2011b). Fine-scale timings of major insect and plant intercontinental dispersals within this interval have not been resolved; however, major pulses of mammal dispersal events have been established either before or after Okanagan Highland times (Woodburne et al., 2009).

Combined with the effects of low seasonality, low diurnal energy fluctuation might provide an explanation for our findings of such high beta diversity (Fig. 1) (see Ghalambor et al., 2006). Modern



**Fig. 6.** Rank abundance plots for (A–E) fossil insect samples from each locality, and (F) modern insects at the La Selva Research Station, Costa Rica ( $n = 432$ ). The Costa Rican site has a hot climate (megathermal,  $\text{MAT} = 26^\circ\text{C}$ ) and the Eocene sites are cooler, varying between upper microthermal to lower mesothermal MAT values (see text). They all, however, share low temperature seasonality. All show a diversity pattern of few common species and many rare species, a commonly recovered tropical diversity pattern. The Costa Rica data are from Archibald et al. (2010), using groups equivalent to those examined in this study: Symphyta (Hymenoptera), Ichneumonidae (Hymenoptera), Diptera, Auchenorrhyncha, and Neuroptera.

**Table 3**  
Numbers of species shared between sites. Abbreviations as in Table 2.

Locality	DC	HR	Mc	Qu
HR	0–2	–	–	–
Mc	0	1–3	–	–
Qu	0	0	0	–
Re	0	3–4	1–7	1–2

**Table 4**  
Sørensen similarity index values between sites. Abbreviations as in Table 2.

Locality	DC	HR	Mc	Qu
HR	0–0.02	–	–	–
Mc	0	0.01–0.03	–	–
Qu	0	0	0	–
Re	0	0.03–0.04	0.01–0.05	0.01–0.02

tropical montane seasonal temperature variation is very low, whereas Temperate Zone high elevations receive almost five times more solar radiation influx at noon on midsummer day than on the winter solstice at 50° North and South (Sarmiento, 1986). Diurnal fluctuation, however, is mostly greater in low latitude mountains, where the daily range of temperature minima to maxima is at least 3 to frequently 10 times more than the difference between the warmest and coldest month mean temperatures (Sarmiento, 1986). The daily temperature range is notably narrower in the Alps and Himalayas (Mani, 1968). This greater daily temperature variation in modern tropical mountains is a consequence of the difference between vertical midday insolation and night time high elevation cold increased by accelerated heat loss in the thin air (Mani, 1968; Sarmiento, 1986; Ghalambor et al., 2006), contrasted with the low midday angle of insolation in the Temperate Zone resulting in a lesser diurnal temperature shift. A lower daily fluctuation in the upper mid-latitude Okanagan Highlands combined with low Eocene seasonal temperature range as in the modern tropics implies even less yearly temperature overlap between elevations and even narrower temperature tolerances for its biota relative to modern tropical montane regions, increasing both of these factors that Janzen proposed would promote high beta diversity, creating a 'super Janzen effect'.

Our findings support Janzen's model of a key role for temperature seasonality – and a role of daily temperature fluctuations – in regulating beta diversity across montane regions. Greater extra-tropical montane endemism in the Eocene provides further support for a net loss in global diversity since then. This is the 'pear-shaped Cenozoic' model (Archibald et al., 2010) of early Cenozoic high diversity extending outside the tropics with low to flat latitudinal diversity gradients (Archibald et al., 2010; Rose et al., 2011), declining to the modern pattern of high diversity restricted to the tropics in association with the later Cenozoic development of extra-tropical seasonal climates. It appears that mountain passes – and global biodiversity – were higher in the Eocene.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2012.10.043>.

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