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Abstract.—In the modern world, biotic diversity is typically higher in low-latitude tropical regions where there is abundant insolation (light and heat) and low thermal seasonality. Because these factors broadly covary with latitude, separating their possible effects on species diversity is difficult. The Eocene was a much more equable world, however, with low temperature seasonality extending into lower-insolation higher, cooler latitudes, allowing us to test these factors by comparing insect species diversity in (1) modern, temperate, low-insolation, highly seasonal Harvard Forest, Massachusetts, U.S.A., 42°29′N; (2) modern, tropical, high-insolation, low-seasonality La Selva, Costa Rica, 10°26′N, and; (3) Eocene, temperate, low-insolation, yet low-seasonality McAbee, British Columbia, Canada, above 50°N paleolatitude. We found insect diversity at McAbee to be more similar to La Selva than to Harvard Forest, with high species richness of most groups and decreased diversity of ichneumon wasps, indicating that seasonality is key to the latitudinal diversity gradient. Further, midlatitude Eocene woody dicot diversities at McAbee, Republic (Washington, U.S.A.), and Laguna del Hunco (Argentina) are also high, similar to modern tropical samples, higher than at the modern midlatitude Harvard Forest. Modern correlations between latitude, species diversity, and seasonal climates were established some time after the Eocene.

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Introduction

G. E. Hutchinson (1959) asked, Why are there only two species of the insect *Corixa* in a Sicilian pond, not 20 or 200? What governs global patterns of diversity? The dramatic increase in species diversity toward the equator (with few notable exceptions, e.g., ichneumon wasps [Janzen 1981], aphids [Heie 1994]) is one of the most striking large-scale biotic patterns in the modern world (Dobzhansky 1950; Fischer 1960; Pianka 1966; Stevens 1989; MacArthur 1972; Rohde 1992; Gaston 2000; Willig et al. 2003). In the mid–twentieth century, Dobzhansky (1950) discussed our limited understanding of the causes of this phenomenon as a long-standing problem; indeed, it has been noted for at least two centuries (von Humboldt 1808; Darwin 1845; Hawkins 2001). The number of studies has risen dramatically in recent decades, as have explanatory hypotheses—at least 120 by one count—yet consensus remains elusive; some have proven difficult to test, others controversial (Rohde 1992; Palmer 1994; Currie et al. 1999; Willig et al. 2003). They broadly focus on (and some mix) history, geography, and climate, the three fundamental factors by which the tropics and extra-tropics differ (for detailed reviews, see above references).

Is the modern latitudinal diversity gradient a fixed, fundamental, and enduring condition; or is it a recent expression governed by labile factors, with other patterns expressed through geologic time? Proposed explanatory factors have all changed through the Phanerozoic: continental and oceanic configurations with associated orogenies and changes in sea level; and changes in albedo, and in atmospheric and oceanic circulations, affecting heat and moisture distribution (e.g., Barron

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1981; Crame and Rosen 2002; Shellito and Sloan 2006). A persistent, modern latitudinal gradient through the Phanerozoic would then strongly suggest rejection of all current hypotheses.

Recently, historical and geographic hypotheses explaining the diversity gradient have been strongly challenged (see below), suggesting that climate-based explanations may prove a more fruitful avenue of research (for reviews of climatic hypotheses, see Pianka 1966; Rohde 1992; Gaston 2000; Willig et al. 2003). Here, we examine diversity relative to climate, and focus on those climatic factors that differ with latitude: insolation (light and heat) and thermal seasonality. Separating their effects on diversity has proven largely problematic in modern-world settings owing to their broad covariance, although intriguing possibilities do exist (see Northern versus Southern Hemisphere, below).

The global climatic regime where low thermal seasonality is primarily associated with high equatorial insolation and associated high mean annual temperature (MAT) is relatively recent in geological time (Greenwood and Wing 1995; Zanazzi et al. 2007; Zachos et al. 2008). Eocene biotic assemblages that mix cool-associated taxa with those now restricted to the tropics indicate a climate of mild winters without significant frost days even into mid- and higher-latitude regions with cooler MAT (Daley 1972; Greenwood and Wing 1995). Insect assemblages from Eocene Baltic amber, the Bembridge Marls of the Isle of Wight, and others combine both modern boreal and tropical taxa (Archibald and Farrell 2003). At least some plant taxa with mutually exclusive climatic tolerances in a modern world setting are found together in almost all western North American early Eocene floras (Wing 1987). Organisms now restricted to the tropics such as palms, crocodilians, large (non-burrowing) tortoises, and thermophilic mammal and insect taxa ranged into high-latitude regions of far cooler MAT than they do today, in some cases into the high Arctic at 78°N paleolatitude (Estes and Hutchinson 1980; McKenna 1980; Wing 1987; Wing and Greenwood 1993; Markwick 1994; Greenwood and Wing 1995; Archibald and Farrell 2003; Jahren 2007). Possible lack of winter hardening in wood from the Arctic Eocene of Axel Heiberg Island (Basinger 1991; Jahren 2007) and conifers with frost-intolerant nearest living relatives from the late Paleocene or early Eocene of Spitsbergen (Schweitzer 1980; but see Wolfe 1980) also suggest minimal if any freezing days at high, cool paleolatitudes. Eocene Kamchatka had temperate and thermophilic floral elements such as palms (Budantsev 1992; for other Eocene high-latitude palm occurrences, see Greenwood and Wing 1995). Palms reached into the high Arctic at least at times during the early Eocene, indicating coldest month mean temperatures of >8°C at ~85°N paleolatitude (Sluijs et al. 2009). The London Clay flora includes 11% temperate and 43% exclusively or mainly lowland tropical taxa (Reid and Chandler 1933; Daley 1972). Australia, farther south in the Eocene, has localities that were without significant frost days at MAT <15°C and supported thermophilic taxa such as palms and crocodiles (Greenwood and Wing 1995). The Eocene world in which such groups lived well outside their modern low-latitude ranges under globally low-seasonality climatic conditions was described as a ''lost paradise'' by Shellito and Sloan (2006).

Such an equable climate in a temperate MAT setting existed in early Eocene forests of the Okanagan Highlands, extending ~1000 km through southern British Columbia, Canada, and northern Washington, U.S.A. (Greenwood et al. 2005), sustaining a tropical/temperate mixture of insect and plant taxa (Erwin and Stockey 1990; Hopkins and Johnson 1997; Wehr and Manchester 1996; Archibald and Mathewes 2000; Labandeira 2002; Archibald and Farrell 2003; Greenwood et al. 2005; Moss et al. 2005). The McAbee site in the central Okanagan Highlands is particularly noted for its exceptionally rich, well-preserved insect assemblage.

Here, we answer Erwin's (2009) call to examine the processes governing patterns of biodiversity by looking into deep, geologic time, consistent with Harrison and Cornell (2007), who argued that efforts to understand patterns of diversity relative to climate would profit from including fossil and paleoclimatic evidence. We evaluate the possible roles of climatic factors in generating the latitudinal gradient of species diversity by comparing insect diversities in three settings that allow their separate evaluation: (1) the Harvard Forest Ecological Research Site, Massachusetts, U.S.A., a modern, temperate forest with midlatitude insolation, cool MAT, high seasonality at 42°29′N; (2) La Selva Biological Station, Costa Rica, a modern, tropical forest with low-latitude insolation, high MAT, and low seasonality at 10°26′N; and (3) the Okanagan Highlands site at McAbee, British Columbia, Canada, an Eocene, temperate forest with midlatitude insolation, cool MAT, yet low seasonality above 50°N paleolatitude. We further assessed our results in relation to the record of Phanerozoic latitudinal diversity gradients and to Blackburn and Gaston's (1996a) question: Is high tropical species richness or low extratropical species richness the ''normal'' state? Finally, we consider the implications of our results for large-scale Cenozoic patterns of biodiversity.

Hypotheses Explaining the Current Latitudinal Biodiversity Gradient

Historical Hypotheses

According to the Pleistocene disturbance hypothesis, diversity in extratropical regions has not yet recovered from the effects of glaciation (Fischer 1960). However, many ranges appear consistent with the effects of modern climatic factors; although traces of the effects of glaciation on diversity may be detectable in some portions of North America, post-glacial diversity may be mostly stabilized, its effects erased (Simpson 1964; Adams and Woodward 1989; Roy et al. 1998; Silvertown 1985; Currie 1991; Francis and Currie 2003; Hawkins and Porter 2003; Hawkins 2004).

Alternatively, Pleistocene episodic global cooling, eustatic sea-level drop, and glacial sequestering of water might have resulted in tropical rainforest fragmentation, producing isolation of populations and consequent pulses of allopatric speciation (Haffer 1969, 1997). However, a number of lines of evidence are inconsistent with this, e.g., biotic ranges that conflict with expectations based on proposed refugia, and older molecular divergence times (Cracraft and Prum 1988; Nelson et al. 1990; Moritz et al. 2000; Whinnett et al. 2005; Bonaccorso et al. 2006; McKenna and Farrell 2006; Anthony et al. 2007). Palynological data indicate continuous forest since at least the Miocene (Hoorn 1997; Colinvaux and De Oliveira 2001), and results of sediment analyses putatively supporting refugia have alternative explanations (Colinvaux et al. 2000; Colinvaux and De Oliveira 2001; Kastner and Goñi 2003).

Geographic Hypotheses

The mid-domain effect hypothesis is that the diversity gradient results from the geometry of Earth and its landmasses independent of environment or history (Colwell and Hurtt 1994; Colwell and Lees 2000). However, when tested against observed diversity patterns, or including longitude as well as latitude, the hypothesis produces many equivocal or contradictory results, and some of its assumptions appear problematic (Bokma et al. 2001; Zapata et al. 2003, 2005, references therein; but see Colwell et al. 2004a; Currie and Kerr 2008).

The species-ecoclimatic area hypothesis, that species richness diminishes toward the poles as a function of declining area of ecoclimatic zones (Terborgh 1973; Rosenzweig 1995; Rosenzweig and Sandlin 1997), is problematic in that modern tundra covers much more area than other extratropical regions, yet does not have greater diversity (Rohde 1997; Chown and Gaston 2000), and the Northern Hemisphere has 70% of Earth's land area without higher diversity. Individual taxon diversities also conflict with this hypothesis (e.g., see Roy et al. 1998).

Climatic Hypotheses

Two major variables distinguish modern tropical from extratropical climates: high solar energy influx and low thermal seasonality. Insolation, i.e., light (photosynthetically active radiation, or PAR) and heat (ambient, or thermal, energy), decreases with increased latitude owing to sunlight's higher angle of incidence (see discussion by Clarke and Gaston 2006). Mean annual temperature (MAT) is a convenient, often-used proxy for ambient energy. Here, we define temperature seasonality as the ratio of MAT to coldest-month mean temperature (CMMT).

Insolation.—Differential insolation could influence diversity in a number of ways. Higher tropical energy influx promoting greater primary production may result in larger, viable population sizes of specialists, or resulting higher plant diversity could in turn increase diversities of herbivores and trophically dependent taxa (Wright 1983; Srivastava and Lawton 1998; Evans et al. 2005). Insolation, productivity, population densities, and diversity are, however, decoupled in numerous cases (Day et al. 1988; Field et al. 1998; Currie 1991; Adams and Woodward 1989; Rosenzweig 1992; Angel 1993; O'Brien 1993, 1998; Tilman and Pacala 1993; Eggleton et al. 1994; Huston 1994; Huston 2003; Storch 2003). Higher low-latitude ambient energy might promote a wider range of metabolic specialists (endotherms and ectotherms for different reasons) (Clarke and Johnston 1999; Lovegrove 2000, 2003; Clarke 2003, 2004; Anderson and Jetz 2005; Clarke and Gaston 2006).

The diversity gradient might also result from differential tropical extinction or speciation rates (Stebbins 1974; Stenseth 1984; Chown and Gaston 2000; Moritz et al. 2000; Mittelbach et al. 2007), or both (Jablonski et al. 2006; McKenna and Farrell 2006). Higher tropical speciation is supported by vertebrate molecular data (Martin and McKay 2004) and some fossil evidence (Stehli et al. 1969; Hecht and Agan 1972; Crame 2000, 2002; Buzas et al. 2002; Jablonski et al. 2006; but see Leighton 2005). A variety of mechanisms could promote tropical speciation (Bush 1994), e.g., increases in eurytopy (Cracraft 1985; Rosenzweig 1992; Owens et al. 1999), generations per year due to faster development (Rohde 1992; Turner 2004; Clarke and Gaston 2006; but see Cardillo 1999; Whittle and Johnston 2003), mutation, metabolic rate, or population sizes (Allen et al. 2002; Brown et al. 2003, 2004; Evans and Gaston 2005 and references therein; Clarke and Gaston 2006; but see Bromham and Cardillo 2003; Wright et al. 2006).

Seasonality.—Ever since von Humboldt (1808), scientists have used the stable, low thermal seasonality of the tropics to explain their high diversity. Lower-latitude seasonal stability could increase stenotopy, and so population fragmentation and speciation, because climatic change across a mountainous landscape creates larger dispersal barriers than in higher latitudes; this is Janzen's (1967) notion that ''mountain passes are higher in the tropics'' (and see Huey 1978). Or, increased stenotopy could promote smaller ranges (''Rapoport's rule'' [Stevens 1989; Gaston et al. 1998; Gaston and Chown 1999]), with greater opportunity for species overlap between them, although evidence of this is equivocal (Roy et al. 1994; Rohde 1999; Lane 2007; Novotny et al. 2007; Qian et al. 2007; Ruggiero and Werenkraut 2007; Stauffer et al. 2007; Moreno et al. 2008). Low tropical seasonality could allow finer niche gradations, increasing species density (Hutchinson 1959; Klopfer 1959; Klopfer and MacArthur 1960; MacArthur 1972). This is evident in some groups, but not others (Scriber 1973; Rohde 1978; Beaver 1979; Fiedler 1998; Vázquez and Stevens 2004; Novotny et al. 2006; Dyer et al. 2007). Finally, low seasonality could increase the active period, thus increasing number of generations per year and, ultimately, effective evolutionary rate independent of ambient energy level.

Our understanding of the relative roles of insolation (PAR, MAT) and seasonality in determining the present-day latitudinal gradient of species diversity has been hampered by their general covariance with latitude. Cool MAT values are combined with low seasonality today in mountainous regions in the tropics; however, the effects of isolation, limited areas, and high elevation would confound diversity-climate comparisons in such regions. However, less seasonal Southern Hemisphere climates at equivalent latitudes in southern Australia, New Zealand, and South Africa provide intriguing possibilities for examining seasonality and diversity where comparable test sites, without potentially confounding factors such as strong precipitation seasonality, can be identified. A similarity between past equable climates and those of the modern Southern Hemisphere was recognized by Upchurch and Wolfe (1979), who calibrated their Cretaceous leaf physiognomy climate estimation technique to modern Southern Hemisphere climate data.

Platnick (1991) argued that the modern Earth is ''pear-shaped'' in biodiversity, that diversity decreases with latitude more quickly in the Northern than Southern Hemisphere (Blackburn and Gaston 1996a; Chown et al. 2004). Although some taxa, such as aphids and penguins, are mostly or entirely restricted to one hemisphere, greater Southern Hemisphere diversity appears repeatedly, e.g., in spiders, ants (more ant species in Australia than in all the Northern Hemisphere), termites, triatomine bugs, some Lepidoptera, and New World birds (Platnick 1991; Eggleton 1994; Blackburn and Gaston 1996a,b; Gaston and Blackburn 1996; Rodriguero and Gorla 2004; Kristensen et al. 2007; Dunn et al. 2009). There is a distinct decrease in terrestrial vertebrate species diversity with increase in latitude in North America, which is generally not so in Australia (Schall and Pianka 1978). Family-level diversity in mammals and seed plants is higher in the Southern Hemisphere overall (Gaston et al. 1995), and plant species richness declines away from the equator more rapidly in the Northern Hemisphere (Gentry 1988). The Southwest Australia Floral Region (mallee, kwongan, and associated region) has high diversity, with some 7380 native vascular plant species, 49% of which are endemic (Hopper 1979; Hopper and Gioia 2004). The Cape Floristic Province (fynbos and associated region) in temperate southwestern Africa (31°–34°S) has about 8650 species of vascular plants, perhaps 65% endemic, one of the world's richest botanical diversities for its size, similar to the wet tropics (Goldblatt 1997). Both regions have climates characterized by low thermal seasonality (and other attributes: open heath lands, nutrient-poor soils, high fire and grazing disturbance, winter rain), as do the other high-diversity Mediterranean climate floral regions: California (4300 spp., 35% endemic), central Chile (2400 spp., 23% endemic), and the Mediterranean Basin (25,000 spp., 50% endemic), together totaling less than 5% of Earth's land surface, yet with almost 20% of its flora (Cowling et al. 1996).

Productivity and area are unlikely explanations of Southern Hemisphere diversity, as both are higher in the terrestrial Northern Hemisphere (Field et al. 1998). Differential seasonality may be key to understanding pear-shaped diversity patterns. Although seasonality and MAT covary with latitude in both hemispheres, their rates of change with latitude are not equivalent; the extratropical Southern Hemisphere is distinctly less seasonal than its Northern Hemisphere counterpart (Fig. 1) (Greenwood and Wing 1995; Gaston and Chown 1999: Fig. 1; Chown et al. 2004: Fig 1). Rapoport's rule, causally linked to seasonality, is largely a Northern Hemisphere phenomenon, although it should be noted that there are relatively fewer Southern Hemisphere studies (Rodhe 1996; Gaston et al. 1998). Darwin (1845: pp. 242–245, 250–251) proposed such a link between seasonality and diversity; commenting on the more equable climate throughout the Southern Hemisphere, he speculated that ''as a consequence, the vegetation partakes of a semi-tropical character'' and the temperate native forests in Chile ''almost rival in luxuriance those of the glowing intertropical regions.''

Southern Hemisphere insects rarely have cold-related diapause; they have different strategies than Northern Hemisphere insects for surviving winter temperatures (Addo-Bediako et al. 2002; Sinclair et al. 2003; Chown et al. 2004). In the Northern Hemisphere, most insects are either freeze avoiding (reducing their freezing point) or strongly freeze-tolerant, with extended preparation and recovery times for both. In the Southern Hemisphere, moderate freeze tolerance is predominant, necessitating less time in preparation and emergence (Sinclair et al. 2003; Chown et al. 2004); moreover the lower lethal temperature for insects and the temperature at which ice crystals form decrease less with latitude than in the Northern Hemisphere (Addo-Bediako et al. 2000).

Alpine treeline appears to be associated not with CMMT, but with warm-month mean

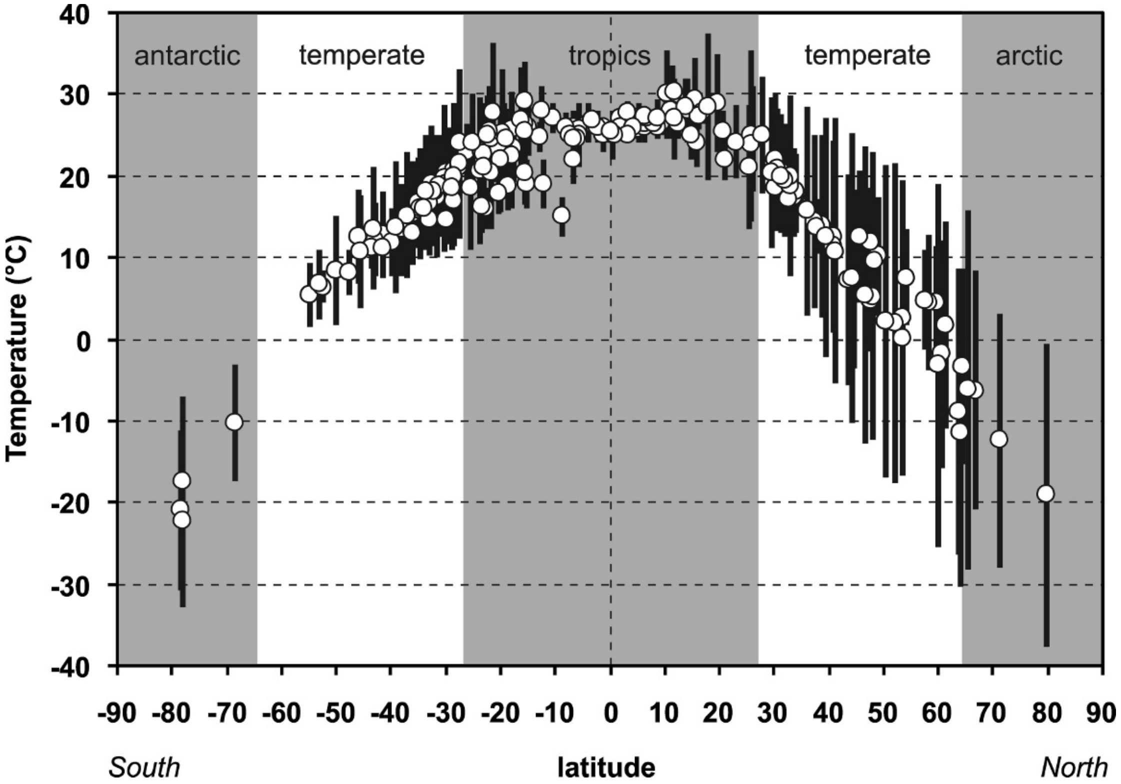

FIGURE 1. Terrestrial seasonality (black lines), mean annual temperature (circles), and latitude. The data set includes east coast, west coast, and continental interior transects from South and North America, Africa, Europe, Antarctica, and Australia. The gap in the Southern Hemisphere data is from latitudes between Antarctica and South America and Australia. Data from compilation presented by Greenwood and Wing (1995).

temperature (WMMT), which controls wood production. The treeline is at similar elevations in both Northern and Southern Hemisphere regions of equivalent WMMT, despite lessened CMMT in the Southern Hemisphere (Jobbágy and Jackson 2000). Plant taxa have varying cold-hardiness strategies (Sakai and Larcher 1987), and seasonality controls the character of treeline forests globally. With increasing seasonality, treeline forests go from dicot- to conifer-dominated. Northern Hemisphere treelines tend to be dominated by needle-leaved conifers (Pinaceae), and Southern Hemisphere by dicots (*Nothofagus* spp., and also *Eucalyptus* spp.), with broadleaf conifers only locally important (Araucariaceae, and Podocarpaceae).

Although there are examples of differential diversity patterns in southern oceans (Poore and Wilson 1993; Rex et al. 1993; Brey et al. 1994; Clarke and Crame 1997; Crame 2000; Gray 2001, but see Chown et al. 2004; Hillebrand 2004; Brandt et al. 2007; Waller 2008), marine diversity patterns often appear complex, at times obscure and difficult to interpret (Clarke 1992; Rohde 1992; Dauvin et al. 1994; McAllister et al. 1994; Gaston 1996; Clarke and Crame 1997; Roy et al. 1998; Clarke and Lidgard 2000; Roy et al. 2000; but see Hillebrand 2004).

Materials and Methods

Localities Sampled.—For La Selva and Harvard Forest, MAT, CMMT, and mean annual precipitation (MAP) data were available from on-site weather stations. For McAbee, these were estimated using two paleobotanical proxies of climate; taxon-independent leaf margin analysis (LMA) and taxon-dependent nearest living relative (NLR) bioclimatic analysis (Kershaw 1996; Wilf 1997; Greenwood et al. 2005).

Temperate zone insect samples were collected by a pond in the second-growth eastern deciduous forest at Harvard Forest, near Petersham, Massachusetts, U.S.A., 42°29′N latitude. MAT is a microthermal 7.2°C; CMMT, −7.4°C; and MAP, 107 cm/year (Harvard Forest 2006).

A tropical zone comparative assemblage was collected in the rainforest of the La Selva Biological Station, on the lowland coastal plain by the foothills of the central volcanic mountain chain, northeastern Costa Rica, 10°26′N latitude (McDade and Hartshorn 1994). MAT is a megathermal 25.9°C; CMMT, 24.7°C; and MAP 396 cm/year, with solar radiation, relative humidity, and temperature notably constant throughout the year (McDade and Hartshorn 1994; Sanford et al. 1994).

The McAbee locality is a deposit of early Eocene lacustrine shale about 15 km east of Cache Creek, British Columbia, Canada. New radiometric dating from $^{40}Ar/^{39}Ar$ decay analysis of biotite recovered from tephra intercalated within the shale beds gives an age of 52.90 ± 0.83 Ma (Mortensen and Archibald unpublished data). Modern McAbee is at 50°48′N latitude, but as North America has rotated counterclockwise since the early Eocene (Andrews 1985), its paleolatitude was somewhat more northern, consequently with a midlatitude angle of PAR influx. McAbee MAT is estimated as a microthermal 10.7 ± 2.4°C by LMA, 13.5 ± 2.5°C by NLR; CMMT, 5.8 ± 2.0°C, by NLR; and MAP as 108 ± 35 cm/year by NLR (Greenwood et al. 2005). The presence of palms at McAbee, however, constrains CMMT to >8°C. In the modern world, the sensitivity of their seeds and seedlings to frost restricts palms to regions with CMMT >5°C; but this sensitivity increases to >8°C under conditions of elevated CO_2 as are inferred for the Eocene (Sakai and Larcher, 1987; Greenwood and Wing 1995; Royer et al. 2002; Shellito et al. 2003; Sluijs et al. 2009). Although temperature seasonality was much reduced relative to that in modern similar latitudes, there would have been photoperiod seasonality at this paleolatitude.

Multiple geologic and biotic indicators suggest the Okanagan Highlands was a cool upland (Schorn and Wehr 1994; Greenwood et al. 2005; Tribe 2005). Its forest is modeled as the antecedent of the modern eastern deciduous zone, although it differed in several significant ways, including the coexistence of cool and thermophilic biota (see above; Archibald and Farrell 2003; Greenwood et al. 2005).

Insect Sampling.—Sampling strategy for extant insects was designed to correspond as closely as possible to putative taphonomic sorting of fossil samples. Insects were collected at La Selva and Harvard Forest with Townes-style Malaise traps, which sample flying insects. Harvard Forest was sampled during a week in August 2004 and a second week in June 2005. The La Selva sample has nine subsamples collected over a two-week period in September 2004, mostly across a successional plot series. Malaise traps were set under open sky, collecting from various forest levels as is assumed would be the case for the fossil sample. An unbiased sample of all specimens recognizable as insect (including fragmentary and poorly preserved) was collected at McAbee, mostly by two workers in 22 days of fieldwork in 2000 and 2001.

Only adult, winged insects were counted. The fossil assemblage consists almost entirely of these, presumably a result of selection by aerial transport to the lake surface; the few others found (e.g., juveniles, worker ants) were excluded from this analysis. Many specimens were preserved as disarticulated wings, so mostly forewing characters were used in determining fossil taxa; isolated hind wings were only used in taxa where they can be confidently separated from or associated with forewings designated to species. We counted extant insects above 2 mm long, a size based on the smallest sizes of fossils. Some families of small (but >2 mm) nematoceran Diptera with delicate wings were excluded (e.g., Chironomidae); they do not appear in the fossil assemblage (but Mycetophilidae does, and was counted).

Floating time is presumed to have been a major taphonomic sorting factor of insects in lacustrine depositional settings, extension of which increases chances of predation, decay, and transport to shore (Martinez-Delclòs and Martinell 1993; Wagner et al. 1996). It differs among insect orders in association with their characteristic ratios of surface area to mass (SM index). Some high SM index insects have water-repellent, ''self cleaning'' wing surfaces, with scales, hairs, or microsculpting that increase adhesion to surface tension (Wagner et al. 1996). For example, butterflies and moths (Lepidoptera) constitute an extreme case—their scaled wings and high SM index extend floating time to the point of unrecognizable decomposition in actualistic aquarium studies (Martinez-Delclòs and Martinell 1993; Wagner et al. 1996). No Lepidoptera were found in the fossil sample, likely due in at least part to this characteristic, and for this reason, this order was excluded from analyses in the modern samples.

McAbee has, however, a strong representation of Neuroptera, which have water-repellent wings and a high SM index (but not as high as Lepidoptera). They are absent or rare in most Paleogene localities, indicating a process in operation at McAbee alleviating the effects of these factors (Archibald and Makarkin 2006). This may have been a consequence of annual diatom blooms, as proposed for late Eocene lacustrine shales at Florissant, Colorado (Harding and Chant 2000; O'Brien et al. 2002). There, diatom blooms may have acted as large sticky traps on or near the surface, collecting insects and lessening their sorting. This entrapment in diatom mucus mats would prevent drift to shore and predation while floating and in the water column; on the substrate it would provide immediate cover, protect against scavenging, and promote growth of biofilms associated with early stages of diagenesis. As is the case at Florissant, the McAbee shale is composed of varve couplets of alternating diatomaceous and sapropel laminae (Mustoe 2005; Wolfe and Edlund 2005).

Diatom blooms may not only have increased fidelity of the fossil assemblage to community assemblage, but also restricted it to the discrete time during annual blooms, likely several months of spring/summer (e.g., Arhonditsis et al. 2003), defined at McAbee more by photoperiod seasonality rather than its low temperature seasonality. The McAbee assemblage would, therefore, be a seasonal, rather than a yearly assemblage, rendering it comparable with the seasonal extant Harvard Forest and La Selva samples. Reworking and mixing of specimens by bioturbation may affect such robust fossils as bivalves, pollen, and organisms preserved in amber (Behrensmeyer et al. 1992), but this is not an issue here with insect fossils in shale, as they (and their wings in particular) are delicate and incapable of surviving reworking or mixing. Their preservation in finely laminated lacustrine shale deposited in quiet, anoxic bottom waters lacking ichnofossil evidence of bioturbation is also evidence for the absence of mixing. The McAbee Eocene forest around the lake remained essentially unchanged over the time interval that the insects were deposited, as the same palynomorph assemblages were detected in a vertical stratigraphic sample series that included the layers sampled for insects (Moss et al. 2005). These data imply that the same community of organisms occupied this forest over the time period sampled by the fossil insect assemblage that we studied here (i.e., repeated samples of the same insect community).

Taxon losses in sampled assemblages relative to the diversity of the source community are confidently greater in the fossil sample than in extant Malaise trap samples, rendering sampled fossil diversity a minimum relative to the extant samples.

Insects were separated to morphospecies, with key orders checked by specialists (see ''Acknowledgments''). In some fossil taxa, large numbers of similar wings were evaluated by comparing ratios of character measurements with variation found within and among extant closely related known species (see online supplemental material at http://dx.doi.org/10.1666/09021.s1). Parataxonomists can separate arthropod samples to morphospecies that closely match orthotaxonomic species as subsequently determined by experts (Oliver and Beattie 1993). Because many more characters were available in extant insects, bias is toward underestimating fossil diversity relative to extant.

Analyses.—The three community samples were compared using rarefaction and Fisher's α index. Fisher's α takes into account both species richness and evenness (Fisher et al. 1943; Gotelli and Colwell 2001; Colwell et al. 2004b; Magurran 2004). A variety of other diversity indices were calculated, such as Chao, Simpson's D, and Shannon's H (Hayek and Buzas 1996), but were found to be more sensitive to sample size than Fisher's α here. Rarefaction further allows meaningful comparison of diversity from data sets of differing sizes (Gotelli and Colwell 2001; Colwell et al. 2004b). To compare rarefaction curves, we took advantage of the fact that for any number of specimens, the species number along the rarefaction curve is normally distributed, with an easily estimated standard deviation (Colwell et al. 2004b). Two curves differ for a particular number of specimens at approximately $p < 0.05$ by the t-test if the number of species for one at that point, minus its standard deviation, is greater than the number of species for the other plus its standard deviation.

McAbee LMA estimates were determined using regression equation (2) of Greenwood et al. (2005), with the error determined as by Wilf (1997). Nearest living relative (NLR) bioclimatic analysis (Kershaw and Nix 1988; Kershaw 1996; Moss and Kershaw 2000; Greenwood et al. 2003; Greenwood et al. 2005) is very similar to the coexistence approach of Mosbrugger and Utescher (1997). The bioclimatic analysis method used the climatic values associated with the distributions of modern plant genera, the nearest living relatives (NLRs) of those found in the McAbee megaflora. A library of climatic profiles (NLR values of MAT, MAP, and CMMT) was produced for key taxa using data on the climate ranges of extant plant genera and individual species from Thompson et al. (1999) and the PALAEOFLORA database (Mosbrugger and Utescher 1997; T. Utescher personal communication 2007). The zone of overlap for a set of NLRs defined the most likely range of values, or coexistence interval (Kershaw and Nix 1988; Kershaw 1996; Mosbrugger and Utescher 1997; Greenwood et al. 2003). Mean values were calculated by examining the climatic variables for each NLR taxon identified in a sample (fossil or extant). The zone of overlap was calculated using the 10th percentile (lower limit) and 90th percentile (upper limit) to deal with outliers (further detail see Greenwood et al. 2005). For further discussion of paleoclimatic analysis, see online supplemental material.

Results

A total of 6045 specimens were identified to 2049 species from the three assemblages. Orders are analyzed here as large morphological, taphonomic, and phylogenetic natural units with plentiful specimens. The most abundant orders in all three samples (excluding Lepidoptera) were Coleoptera, Hemiptera, Diptera, and Hymenoptera, further suggesting that the fossil and extant samples are reasonably comparable. These orders constitute 91% of the McAbee, 98% of the La Selva and 96% of the Harvard Forest samples.

Rarefaction (Fig. 2) clearly shows Coleoptera to be more diverse at La Selva than at Harvard Forest as expected, their curves separating by two standard deviations as sample size increased between 20 and 30 specimens. McAbee Coleoptera are also clearly more diverse than those at Harvard Forest. Although the McAbee Coleoptera curve lies within one standard deviation of the La Selva curve, it appears to trend toward higher diversity; its Fisher's α value is almost double that of La Selva.

The La Selva Hemiptera show distinctly greater diversity by rarefaction than do those from Harvard Forest (Fig. 2), the curves diverging near 50 specimens sampled. McAbee is indicated to be more diverse than Harvard Forest at a sample size around 35. Although the difference between McAbee and La Selva diversity is not statistically different at the end of the McAbee curve, the apparent trend suggests that McAbee would show higher diversity than La Selva with more specimens. Fisher's α value indicates that the McAbee and La Selva samples are similar in diversity and both are much more diverse than that of Harvard Forest.

Rarefaction shows the Diptera at La Selva to be more diverse than at Harvard Forest, their curves separating at about 50 specimens sampled (Fig. 2). Although the McAbee Dip-

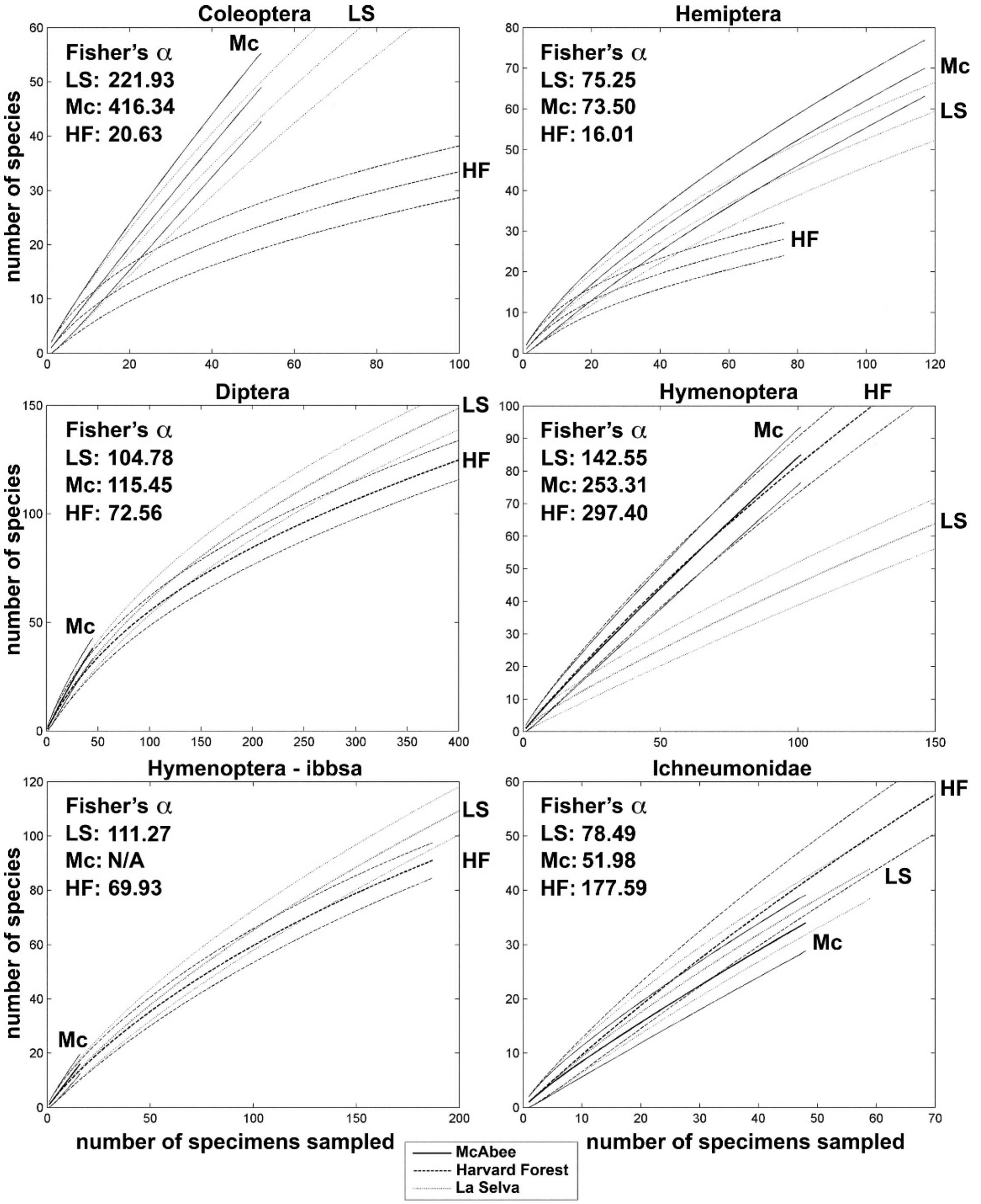

FIGURE 2. Rarefaction curves and Fisher's α values for the orders Coleoptera, Hemiptera, Diptera, and Hymenoptera; the order Hymenoptera without ichneumonids, braconids, bees, sawflies, or ants ("- ibbsa," see text); and the hymenopteran family Ichneumonidae. Three lines in rarefaction curves for each sample indicate the mean and a standard deviation from the mean on either side. LS, La Selva; Mc, McAbee; HF, Harvard Forest.

tera are statistically inseparable from the other samples at the sample size tested, it appears to show a meaningful trend toward being more diverse than the other two samples. This supposition is supported by Fisher's α values, which show diversity at McAbee and La Selva to be close and much higher than at Harvard Forest.

Rarefaction (Fig. 2) and Fisher's α index also indicate that diversity in Hymenoptera is roughly equivalent at McAbee and Harvard Forest, and both sites are significantly more diverse than La Selva. This counterintuitive result may be a product of the complexity of latitudinal diversity patterns within the order and of sampling effects particular to ants. Although most groups of Hymenoptera are more diverse in the tropics, sawflies (Symphyta), Ichneumonidae, Braconidae, and bees are not (Janzen 1981; Michener 1979; Noyes 1989; Kouki et al. 1994; Gauld and Gaston 1995). Further, the mass release of ants in mating flights near some La Selva traps flooded them with winged reproductives (428 specimens of *Ectatomma* sp. 1 and 171 specimens of *Hypoponera* sp. 2). In the McAbee sample, sawflies and Ichneumonidae dominate the Hymenoptera, together with a few Braconidae constituting 78% of those specimens identifiable to species, or 84% including ants. There are no bees in the McAbee sample, but they are well represented in the larger La Selva and Harvard Forest samples, where ichneumonids and sawflies were smaller components (see online supplementary material, Table 3).

To test the effects of these taxa on the Hymenoptera analysis, we made separate ''Hymenoptera-ibbsa'' data sets excluding ichneumonids, braconids, bees, sawflies, and ants. (The specimens of the several non-hymenopteran taxa that are also most diverse in temperate regions, e.g., aphids, were so few that we did not separate them in analyses of their orders.) The two extant samples showed predicted results with this modified data set; the La Selva rarefaction curve is almost separated from the Harvard Forest curve, strongly trending toward greater diversity (Fig. 2). The La Selva Fisher's α value is far greater than that for Harvard Forest. In the McAbee sample, only 16 specimens with 16 species remained in the modified data set, leaving its analysis without meaningful results.

Ichneumonidae are well represented in all samples (La Selva, 44 specimens; Harvard Forest, 199; McAbee, 48). The Ichneumonidae data set was analyzed to test its influence on the Hymenoptera analysis. The rarefaction was inconclusive within two standard deviations (Fig. 2), although Harvard Forest appears strongly trending toward greater diversity than La Selva and McAbee given sample sizes tested. The La Selva and McAbee Fisher's α values are both small relative to Harvard Forest, indicating that the McAbee Ichneumonidae sample is distinctly more similar to the La Selva sample, with the Harvard Forest sample most diverse. These results are consistent with previous findings of highest diversity of Ichneumonidae in the temperate zone (Janzen 1981).

The remaining orders, represented by small numbers of specimens, were combined with those above as a composite ''All'' data set containing all insects determined to species. Rarefaction showed the La Selva insects clearly separated as more diverse than Harvard Forest insects at around 1500 specimens sampled. Rarefaction separated McAbee as significantly more diverse even than La Selva at 200–300 specimens (Fig. 3). Fisher's α values indicate that McAbee and La Selva diversities are greater than that of Harvard Forest.

An ''All-ibbsa'' data set (the composite data set, excluding Ichneumonidae, bees, Braconidae, sawflies and ants) increased the separation of the La Selva and Harvard Forest rarefaction curves as expected (Fig. 3); both the La Selva and McAbee samples significantly diverged from Harvard Forest at around 150 specimens sampled. Although McAbee does not separate from La Selva by two standard deviations, it does appear to trend toward greater diversity. Fisher's α values also indicate that diversities at McAbee and La Selva are greater than at Harvard Forest.

Discussion

Eocene McAbee insect diversity was higher than present-day temperate Harvard Forest, and similar to, or for some taxa possibly higher than, present-day tropical La Selva, despite all factors operating to result in lower observed relative diversity in the fossil sample: (1) greater loss of taxa through taphonomic processes; (2) lower resolution

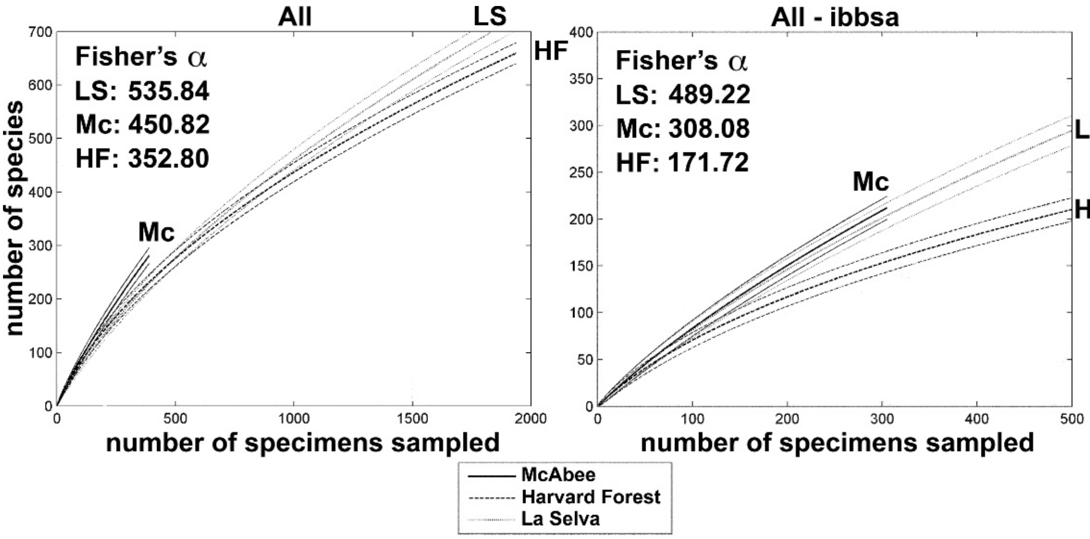

FIGURE 3. Rarefaction curves and Fisher's α values for the data set ''All'' of all insect species and the ''All - ibbsa'' data set (the ''All'' data set without ichneumonids, braconids, bees, sawflies, or ants; see text). LS, La Selva; Mc, McAbee; HF, Harvard Forest.

in taxonomic determination due to preservation; and (3) higher elevation. The pattern of similar diversity at McAbee and La Selva, both distinct from Harvard Forest, was seen not only in increased species richness of most groups, but also in decreased diversity of Ichneumonidae. Preliminary data from taphonomically equivalent samples of fossil leaves and leaf litter (current research) suggest that McAbee also had high plant diversity, also comparable to that of the modern tropics and much higher than modern temperate forests such as Harvard Forest; the data further suggest that McAbee floral diversity is typical of other midlatitude Eocene sites such as the Okanagan Highlands site at Republic, Washington, U.S.A., and the Argentinean Laguna del Hunco (Fig. 4). Laguna del Hunco was considered by Wilf et al. (2003, 2005a) to have the highest diversity of known Eocene macrofloral sites.

Although these findings show high species richness at higher latitudes prior to Pleistocene glaciation, consistent with the historical disturbance hypothesis, we reject this explanation for reasons given above.

Our results are contrary to what the mid-domain effect hypothesis would predict, as the McAbee was in a continental/latitudinal position that today has lower diversity. They also disagree with differential insolation as an explanation, as PAR influx at Eocene McAbee would have been at the oblique angle of the higher temperate zone (paleolatitude above 50°N), and ambient energy was temperate, with microthermal MAT; nonetheless, we see a similar pattern of insect diversity there as in modern megathermal Costa Rica with low angle of incidence insolation, high PAR, and high MAT.

These findings imply that the latitudinal gradient of species diversity is driven by seasonality (although absolute values of CMMT may still control the presence of particular lineages below a threshold, and many other factors may locally attenuate diversity such as low moisture or nutrient availability, or extended darkness in highest latitudes). Below we discuss a variety of possible mechanisms by which low seasonality may have generated high McAbee insect diversity.

Species-Ecoclimatic Area.—Terborgh (1973) defined the ecoclimatic zones concept relative to MAT and MAP. If we replace MAT with seasonality and associated CMMT, then the Eocene world was all or almost all one zone: the low seasonality, no severe frost zone with a tropical/temperate (in the modern sense) mix of biota (Wing and Greenwood 1993;

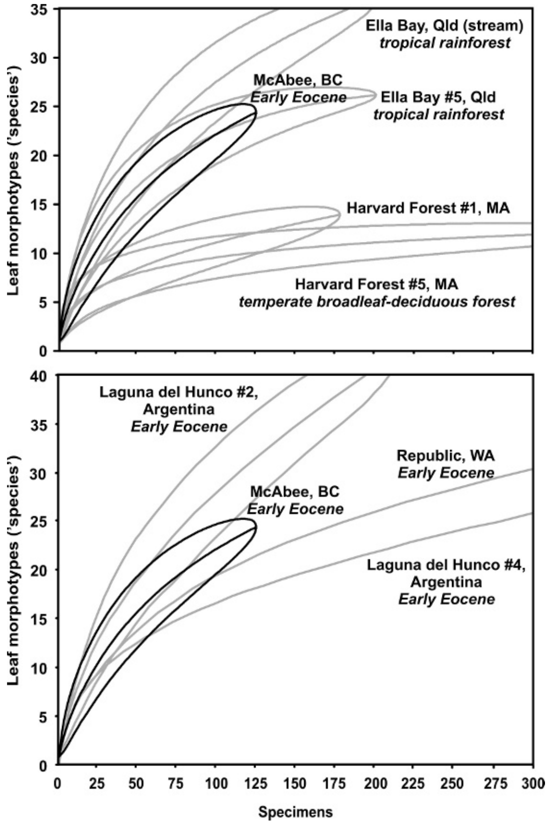

FIGURE 4. Plant diversity (dicot leaf morphotypes) from Eocene temperate McAbee compared with leaf litter samples from other localities. Top, Modern temperate forest (Harvard Forest, Massachusetts) and lowland tropical rain forest (Ella Bay, Queensland, Australia; latitude 17°29′S). Bottom, Other early Eocene midlatitude floras at Republic (Washington, U.S.A.) and Laguna del Hunco (Argentina). Laguna de Hunco and Republic data from Wilf et al. 2003. Extant samples are of forest floor litter, except Ella Bay (stream bed); the Harvard Forest curve is from new data, and Ella Bay is partially from Greenwood (2005). The Harvard Forest and Ella Bay curves represent, respectively, the most and least diverse samples taken from each of those sites; the Laguna del Hunco #2 and #4 samples respectively represent the most and least diverse of those published by Wilf et al. (2003). Graphs present 95% confidence intervals for means, except for Republic and Laguna del Hunco #4 (not provided by Wilf et al. 2003).

Greenwood and Wing 1995; Archibald and Farrell 2003; Shellito and Sloan 2006; Jahren 2007), the extreme size of which would result in high diversity over much of the globe. However, owing to the difficulties mentioned above, this is not a probable explanation.

Plant-Diversity-Driven Insect Species Richness.—It is possible that a high diversity of plants stimulates high diversity of phytophagous, and consequently predatory, parasitic, parasitoid and saprophagous insects. As above, preliminary evidence from current research indicates that plant diversity at McAbee was also high, comparable to tropical rather than temperate levels (Fig. 4). Wilf et al. (2006) found decoupled plant and insect diversities in early Paleocene Montana as indicated by types of insect feeding damage on leaves; however, they interpreted this as evidence of an anomalously unbalanced food web during recovery from the K/T mass extinction event. Rich Eocene plant-insect interactions were shown by highly diverse insect ichnofossils and macroflora at midlatitude Laguna del Hunco, Argentina, implying linkages between insect and plant diversities, which Wilf et al. (2005b) associated with climatic factors.

Speciation Rate by Generations per Year.—Whereas many modern temperate zone insects have one and some two generations per year, tropical insects may have up to 14, a result of increased metabolism, and hence earlier maturity, along with freedom from the limitations of a discrete yearly active period dictated by seasonality (excluding those in regions subject to extreme seasonal precipitation) (Fischer 1960; Bigger 1976; Seger 1983; Hunt and Amdam 2005; Nair 2007). Generation time may be a factor in arthropod evolutionary rate (May 1993), but operating in a complex manner (Fischer 1960; Rosenheim and Tabashnik 1991). McAbee microthermal MAT values indicate no faster insect maturation through acceleration of metabolic rate by high ambient energy; however, lowered seasonality would have reduced or eliminated diapause (in this mesic environment), also allowing for increased generations per year, and so possibly resulting in higher insect speciation rates. This would not, however, account for high Eocene midlatitude plant diversity.

Seasonality-Driven High Primary Productivity.—A longer or continuous growing season promoted by low seasonality could have increased net primary production of the ''temperate/tropical mix'' forest (e.g., palms and spruce together) at higher midlatitude McAbee independent of insolation. Although modern tropical forests show high overall yearly productivity, temperate forests are more productive for each growing season month (Huston 1994). If the temperate forests of the Eocene had primary productivity rates that were comparable but extended throughout the year (even if limited at higher latitudes by photoperiod seasonality), net yearly primary productivity would have been high. As noted above, however, the relationship between primary productivity and diversity remains unclear.

Range Size.—The Okanagan Highlands was the type of low seasonality montane environment that Janzen (1967) envisioned to have ''higher mountain passes,'' and so may have produced fragmented ranges, thus increasing allopatric speciation. Preliminary data from major depositional basins across its 1000 km transect indicate few shared species (Archibald unpublished). Alternatively, lowered seasonality could have created a Rapoport effect (Stevens 1989)—smaller ranges with greater local immigration, generating higher species densities.

Greater Specialization.—Narrowed niche breadth may not be testable with insect body fossils as used in this study, but could well be tested by examining characteristic leaf damage by insect herbivores (e.g., see Labandeira 2002; Labandeira et al. 2002).

The Latitudinal Gradient of Diversity through the Phanerozoic

The modern latitudinal diversity gradient of high tropical species diversity decreasing sharply toward the poles has not been convincingly established for any other time in the Phanerozoic. At times diversity increased toward the paleoequator, but weakly; or a major group increased or decreased with latitude contrary to its modern pattern; or a gradient is undetectable; or there was peak diversity in middle latitudes; or there was a reverse gradient with highest diversity at higher latitudes (references below).

Many of the studies cited below have limitations to be considered. Most use supraspecific taxa, and their results should be interpreted carefully with regard to species diversity patterns. Other examinations pooled data from mixed habitat types/depositional environments or over large spans of time during which major change in geography, climate, and taxon ranges, and major extinction and diversification events occurred (for a discussion of the problem of time-averaging, see Behrensmeyer et al. 1992). Latitudinal diversity patterns in the modern marine realm are often complex and difficult to interpret (see above); interpreting those through the Phanerozoic appears even more daunting.

Paleozoic.—There was a weak latitudinal diversity gradient of Ordovician marine invertebrates (high paleolatitude bin, >30° north or south, and low <30°) (Alroy et al. 2008). Devonian goniatite ammonoid genera show higher diversity in low latitudes. These data, however, may be somewhat confounded by postmortem drifting; the known life range of *Nautilus*, their modern analogue, is in the Australia/Borneo/Philippines region, yet their shells have been found as far as Africa and Japan (House 1973). Further, these data combine occurrences spanning the whole of the Devonian, time-averaging over some 57 million years; and the possible confounding influence of depositional environment bias was not addressed (Cecca et al. 2005; and see below). Limited evidence tentatively suggests that Middle to early Late Devonian plants had less diversity in higher than in lower latitudes (Edwards 1989).

Early Carboniferous (Tournaisian, Visean) foraminifer and bryozoan faunas were broadly cosmopolitan, with relatively minor latitudinal diversity gradients (Ross and Ross 1985). Tournaisian brachiopods show a steep latitudinal diversity gradient, but this becomes extremely shallow later in the Carboniferous (Dinantian, Namurian) (Raymond et al. 1989; Kelley et al. 1990; Crame 2001).

Permian brachiopod families show a latitudinal gradient in the Northern Hemisphere (Stehli et al. 1969). However, family-level studies may be misleading; modern beetles, notably species-rich in the tropics, show a very weak latitudinal diversity gradient of families (Gaston et al. 1995). Generic diversity of Permian (Capitanian) brachiopods shows a different pattern: greatest in the northern hemisphere, strongly peaking at about 30°–40°N, and higher in both the northern and southern temperate zones than at the paleoequator (Shen and Shi 2004). Powell (2007) found that latitudinal diversity patterns in brachiopod genera fluctuated in the Carboniferous and Permian in concert with polar glaciation, which he took to indicate climate as the causal factor. Further, periods where the gradient existed are associated with a Rapoport effect of wide ranges in higher latitudes and wide and narrow ranges in lower latitudes, consistent with a prime role of seasonality in the diversity gradient. He found a weak brachiopod genus diversity gradient in the Late Mississippian, collapsing to near absence in the Pennsylvanian, and weak in the Early Permian. An ''antitropical'' distribution pattern (''bitemperate'' at 30°–50°N and S; ''bipolar'' at >50°) apparently extended throughout the Permian in varying degrees of strength in bivalves, brachiopods, and indeed within all major Permian benthic and pelagic invertebrate groups (Shi et al. 1995; Shi and Grunt 2000).

Mesozoic.—Four segments of the Early Jurassic Pliensbachian and Toarcian Ages show a variety of generic diversity gradients of bivalves, ammonites, gastropods, and brachiopods in segments analyzed between Morocco and Greenland: at times a weak decline northward, or with highest diversity mid-transect, but often with little appreciable difference; bivalve diversity actually increased northward in three of four cases, decreasing only negligibly in the fourth (Hallam 1972). In the Late Jurassic Oxfordian age, marine invertebrate diversity from Normandy to Greenland appears controlled by depositional environment, not temperature, with no regular latitudinal diversity gradient (Fürsich and Sykes 1977). In the Late Jurassic (Tithonian), maximum diversity in bivalve genera occurred between 33° and 40°N (Crame 2001, 2002). Gastropods are more diverse in the tropics than in temperate zones in the Early Cretaceous, but by the Campanian–Maastrichtian, this is reversed; however, once again, sampling from differing habitats may have significantly influenced these data (Sohl 1987). An antitropical bivalve element likely persisted from Late Jurassic through Late Cretaceous times (Crame 1986). Maastrichtian bivalve genera show peak diversity between 30°N and 40°N; the tropical diversity value is reduced much further if rudists (an extinct, highly specialized group) are excluded (Raup and Jablonski 1993; Crame 2001). Stehli et al. (1969) show a Northern Hemisphere latitudinal gradient in species of Maastrichtian planktonic foraminifera. A meta-analysis of ammonite generic diversity gradients between lower and middle northern latitudes (10°–45°N) in fine time slices of the latest Jurassic and earliest Cretaceous showed weak higher diversity in lower latitudes; however, paleoenvironment appeared to be the most important factor controlling diversity. Thus these results may be a product of differing depths sampled, rendering conclusions on the effect of latitude difficult (Cecca et al. 2005). Predatory prosobranch gastropods are diverse today, with species and family diversities increasing strongly toward the equator (Taylor et al. 1980). In four Cretaceous time slices sampled from the Albian through Maastrichtian between 10° and 40° latitude (N and S), patterns of family-level diversity were reversed, with a pronounced increase toward the poles.

In the terrestrial realm, equatorial regions were drier during the Mesozoic and early Cenozoic, with plant productivity and diversity globally highest in midlatitudes (Wing et al. 1992). Triassic Gondwanan plant and insect diversities appear to have been significantly higher in mid to high paleolatitudes than in tropical Euramerica (Anderson et al. 1998, 1999). In the Triassic and Jurassic of Eurasia, plant diversity was highest at about 40°N paleolatitude (Ziegler et al. 1993). In the Late Jurassic, low-latitude drier savanna regions with lower plant diversity than wetter midlatitudes had plentiful and diverse dinosaur communities (Rees et al. 2004). Low-latitude early angiosperm vegetation of the Cretaceous was likely xeromorphic with patchy forests (Crane and Lidgard 1989, Spicer et al. 1993). Perhaps the most diverse Maastrichtian floristic regions were between 45° and 65°N paleolatitude (Horrell 1991).

Cenozoic.—Pollen data from swamp and marginal marine samples show an early Paleogene plant diversity gradient in North America stronger than today across three sample regions of pooled localities: the Canadian Arctic, the U.S. Western Interior, and the U.S. Gulf Coast (Harrington 2004). However, many samples analyzed were of indeterminate position above or below the Paleocene/Eocene boundary, and so of indeterminate positions relative to several major diversity changes shown in the U.S. Gulf Coast region through the sampled times. These include a diversity increase in the last ~1 Myr of the Paleocene; a significant extinction event of 20% of the palynoflora at the Paleocene/Eocene boundary; and first occurrences of Eocene taxa and a 38% diversity decrease in the early Eocene (Harrington and Jaramillo 2007). Harrington's (2004) strong diversity gradient is also in conflict with highly diverse plant assemblages and insect feeding damage types on leaves in midlatitude Eocene Argentina (Wilf et al. 2003, 2005b), a highly diverse Paleocene flora in Colorado (Johnson and Ellis 2002), and modern tropical levels of diversity in Northern Hemisphere midlatitude McAbee and Republic (Fig. 4). High plant diversity was present in the Neotropics during the early–middle Eocene, declining at the end of the Eocene into the Oligocene (Jaramillo et al. 2006).

In the early Eocene, high-latitude (Weddell Sea) and low-latitude (equatorial Pacific) deep-sea foraminifera had similar species richness, but during the later Eocene through earliest Oligocene species richness declined in high but not low latitudes, resulting in the development of a latitudinal diversity gradient (Thomas and Gooday 1996). This likely resulted from an increase in high-latitude seasonality rather than change in productivity or MAT, as indicator taxa associated with seasonality appear in high latitudes at this time (Berger and Wefer 1990; Smart et al. 1994; Thomas and Gooday 1996). Eocene molluscs in Pacific coastal North America had high diversity in midlatitudes; in the early Oligocene, however, they became less diverse as thermophilic taxa dropped out (Addicott 1970). Eocene predatory prosobranch gastropod families showed no statistically significant diversity gradient at all (10°–40°N and S) (Taylor et al. 1980).

In the mid-Miocene, there was a shallow diversity gradient in foraminifera between Panama and the Atlantic coastal plain, with the tropical sample 1.8 times greater than the temperate (compared to 2.6 in modern forams) (Buzas et al. 2002). The modern latitudinal gradient of bivalve diversity between Florida and New Jersey is also steep, yet in the Miocene, it is reduced to near absence (Hecht and Agan 1972). There were early–middle Miocene and late Miocene–Pliocene–Pleistocene latitudinal gradients of marine invertebrate diversity (high paleolatitude bin, >30°N and S; low, <30°) (Alroy et al. 2008). In the Miocene, latitudinal diversity among families of predatory prosobranch gastropods (10°–40°N and S) assumed its modern steep gradient, increasing toward the equator (Taylor et al. 1980).

The modern post-glacial equilibrium diversity gradient in European woody plants (40°–70°N) was established around 6000 years ago (Silvertown 1985).

Paradise Lost

What was the end of Shellito and Sloan's (2006) Eocene paradise? The timing and mode of the decline of MAT over the Cenozoic is becoming increasingly evident (Zachos et al. 2008), although much of the character of the increase in extratropical seasonality after the Eocene remains unclear (Zanazzi et al. 2007; Eldrett et al. 2009). An increase in seasonality may have been ushered in during with the rapid drop in global MAT immediately following the Eocene/Oligocene boundary. This major climatic transition from the Cretaceous–early Paleogene ''greenhouse world'' to the current ''icehouse world'' global temperature regime is also associated with large-scale faunal turnover in Europe and North America (Hooker 2000; Zanazzi et al. 2007; Zachos et al. 2008). Major hypotheses explaining this event focus on changes in oceanic heat transport related to the tectonic rifting of Australia and South America from Antarctica (Prothero 1994, and references therein) or a significant drop in atmospheric CO_2 levels (Shellito and Sloan 2006; Zanazzi et al. 2007). Multiple indicators from higher latitudes, however, suggest a smaller decrease in terrestrial MAT around this time, over a longer period (Schouten et al. 2008). Evidence of the degree of increase in seasonality across the Eocene/Oligocene boundary is mixed, with paleofloristic data in northwestern United States and both pollen and geochemical proxies of climate at high latitudes indicating a much greater increase (e.g., Wolfe 1994; Eldrett et al. 2009) than isotope data from the mid-continent (Zanazzi et al. 2007). Data from high-latitude forests in Greenland show that the main change crossing the Eocene/Oligocene boundary was a shift to colder winters, a shift that is most likely to have affected survival of frost-sensitive plant and animal taxa (Eldrett et al. 2009). Increase in extratropical seasonality may have been linked with other climatic/tectonic events during the late Paleogene through Neogene (see review in Crame and Rosen 2002).

A Pear-Shaped Cenozoic

Our findings confirm Darwin's (1845) speculation of a relationship between equable climates and diversity. The Eocene was then a time of low temperature seasonality that reached into highest latitudes; a cosmopolitan mixture of biotas today associated with both low and higher latitudes; high diversity in floras, insects, insect feeding damage types, molluscs, and foraminifera that extended at least into higher midlatitudes. Only near its end did modern latitudinal diversity gradients begin to develop.

A post–early Eocene drop in extratropical diversity to modern levels implies a net loss of global diversity. The Cenozoic saw dramatic radiations in insect groups such as ants, bees, and other derived apocritan Hymenoptera; ditrysian Lepidoptera; brachyceran Diptera; phytophagous Coleoptera; and others (Farrell 1998; Dlussky and Rasnitsyn 2003; Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005; Moreau et al. 2006). These would have to have been more than offset outside of the tropics by loss of species diversity in groups that have since gone extinct, suffered major losses or are now restricted to low latitudes.

It is well established that many supraspecific taxa with wide latitudinal ranges in the Eocene are now restricted to the tropics, e.g., insects and vertebrates (see above); and plants (Latham and Ricklefs 1993; Greenwood and Wing 1995; Collinson 2000). Although some major Cenozoic insect radiations may have begun by McAbee time, we do see evidence that this was not the case for other major groups. For example, although Brachycera dominates Diptera in our modern samples in both species and proportions of individuals, the more primitive Nematocera is more diverse in the McAbee sample. Preliminary results from ongoing work with McAbee and other Eocene fossil assemblages from the Okanagan Highlands suggest that a variety of other insect groups that have low relative diversity today were more diverse then. McAbee had more families of scorpionflies (order Mecoptera) than any continent today (Archibald et al. 2005; Archibald 2005, 2007, 2009, unpublished), and many more species of mecopterans than there are throughout modern British Columbia (Archibald unpublished). Prophalangopsidae was the dominant orthopteran group in parts of the Mesozoic, yet it is relictual today; including specimens in museum collections, it was well represented by a diverse suite of species at McAbee (current research).

Other studies have found similar patterns in other major biotic groups. Despite originations and major diversifications of various plant taxa between the Carboniferous and Eocene, floral diversity was similar at late Paleozoic and early Cenozoic wet floodplain localities examined by Wing and DiMichele (1995), indicating no net effect of evolutionary innovation and niche differentiation on overall diversity. Likewise, an apparent trend of increased marine invertebrate diversity through the Phanerozoic may in fact be an artifact of the rock record, taphonomy, sampling, and analytical methods, despite major radiations of groups that are diverse today (Raup 1972, 1976; Alroy et al. 2001, 2008; Peters and Foote 2001; Smith 2007; McGowan and Smith 2008). New Zealand Cenozoic mollusc genus and species diversities appear constant from the middle Eocene until the Pliocene, when they decrease (Crampton et al. 2006). Our findings and these examples are all consistent with Gould's (1989) view of diversity through time not as a cone-shaped expansion, but as generally bush-shaped, with episodic pruning and blooming contingent on stochastic events.

It is possible that higher speciation rates account for the greater modern diversity in the tropics. Diversity levels were high among the flora of the Eocene Neotropics (Jaramillo et al. 2006) and the flora and insect fauna of the Miocene Neotropics (Van der Hammen and Hooghiemstra 2000; Antoine et al. 2006). These findings, coupled with an increase in or the development of latitudinal diversity gradients by the Miocene, indicate that relatively high tropical speciation rates, if they exist, might be due to a post-Eocene reduction of extratropical speciation rates rather than an increase in tropical rates.

Blackburn and Gaston (1996a) rephrased the question, ''Why are there more species in the tropics?'' as ''Why are there so few species outside the tropics?'' Which state is ''normal'' and which requires explanation: high tropical species richness or low extratropical species richness? Our findings are consistent with low extratropical species richness as an abnormality of the latter part of the Cenozoic, a consequence of the high seasonality outside of low latitudes that was initiated sometime after the early Eocene (Eldrett et al. 2009). We may then live in a pear-shaped world of diversity through the Cenozoic. The answer to Hutchinson's (1959) question of why only two species of the insect *Corixa* were present in his temperate, seasonal, midlatitude Sicilian pond may lie in the high seasonality of the late Cenozoic extra-tropics: in a temperate, equable, midlatitude Eocene pond, there may have been many more.

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