Differential insect and mammalian response to Late Quaternary climate change in the Rocky Mountain region of North America

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**Abstract**

Of the 200 beetle species identified from Rocky Mountain Late Pleistocene insect faunal assemblages, 23% are no longer resident in this region. None of the 200 species is extinct. In contrast to this, only 8% of 73 identified mammal species from Rocky Mountain Late Pleistocene assemblages are no longer resident in the Rockies, and 12 species are now extinct. Since both groups of organisms are highly mobile, so it would appear that their responses to the large-scale fluctuations of climate associated with the last 125,000 years have been considerably different. Most strikingly contrasting with the insects, there are no mammals in the Rocky Mountain Late Pleistocene fossil record that are found exclusively today in the Pacific Northwest (PNW) region. The PNW does have a distinctive modern mammalian fauna, but only one of these, Keen’s Myotis, has a fossil record outside the PNW region, in the eastern and central United States. No modern PNW vertebrate species have been found in any Rocky Mountain fossil assemblages. Based on these data, it appears that there has been little or no mammalian faunal exchange between the PNW region and the Rocky Mountains during the Late Pleistocene or Holocene. This is in stark contrast to the fossil beetle record, where PNW species are a substantial component in many faunas, right through to the late Holocene.

1. **Introduction**

The systematic study of Quaternary insect fossils began in the Rocky Mountain region in the early 1980s (Elias, 1983, 1985, 1988), and has continued since that time. To date, 122 fossil insect assemblages have been analysed from 13 sites, ranging from northern Montana to southern Colorado (Figure 1). These sites have yielded about 300 insect taxa, predominantly beetles (Coleoptera). The sites range in age from about 125,000 years to recent (Table 1). The fossil beetle faunas include 200 taxa identified to the species level, based on the external morphology of their exoskeletons. This is roughly triple the level of diversity of identified species of mammals from Late Pleistocene assemblages in this region, based on data from Faunmap (Graham et al., 2010).

The aim of this paper is to compare and contrast insect and vertebrate distribution shifts in the Late Pleistocene for the Rocky Mountain region. The Rockies form an archipelago of boreal habitat islands, stretching from the true boreal forests of Canada south to the highlands of New Mexico. As such, these montane habitat islands have provided a series of migration corridors for cool- to cold-adapted biota, with the Great Plains on the east and various deserts and other arid regions on the west. Have vertebrates and invertebrates used these migration corridors in similar ways, in response to Late Pleistocene climate change? We now have sufficient fossil data available to begin to make comparisons.

A wealth of fossil data from Quaternary assemblages (summarized in Elias, 2010) has demonstrated that beetles (and probably many other groups of insects that lack substantial fossil records) shift their geographic ranges in response to climatic oscillations. Evidence for large-scale range shifts of this kind has been found in fossil assemblages from Europe (Coope, 1973), Australia (Porch et al., 2009), New Zealand (Marra, 2003), North America (Elias, 1991) and South America (Ashworth et al., 1989). Coupled with this phenomenon, there is little or no fossil evidence of insect extinctions due to Pleistocene glaciations, even in the more sedentary insect groups (Coope, 1978). In fact, the vast majority of species identified from Pliocene and Early Pleistocene deposits in the Arctic represent extant taxa (Elias and Matthews, 2002). Insect migration in response to climate change is not so much a deliberate act to move away from unsuitable environments. Rather, as typifies r-selected biota, most insects have large numbers of offspring, and most of these offspring move away from their point of origin, to minimize competition with their siblings and other members of their species’ local population. When climatic change occurs, this habit of fanning out in all directions once insects reach maturity ensures the survival of those individuals that happen to migrate to regions that still fall within the suitable climatic envelope of their species. Over Quaternary time scales, this phenomenon has made virtual globe-trotters of some beetle species. For instance, a regular member of Pleistocene cold-period faunas in Britain was the dung beetle *Aphodius holdereri*. This species is known today from a handful of localities, all on the Tibetan Plateau (Coope, 1973). Another startling example of this phenomenon is illustrated by the case of the fossil rove beetle, *Micropeplus* *hoogendorni.* Matthews (1970) described this as an extinct species of rove beetle from Pliocene deposits at a site in western Alaska. The fossil specimens were about 5.7 million years old, and Matthews assumed that the species had since become extinct. However, much younger fossil specimens of *M. hoogendorni* have been found in Middle Pleistocene sites in England (Shotton et al., 1993; Parfitt et al., 2005). Finally, the Russian entomologist, Rjabukhin, described a Siberian species, *M. dokuchaevi*, which appears to be synonymous with *M. hoogendorni* (Elias, 2010). So this tiny beetle has circumnavigated the mid- to high latitudes of the Holarctic region during the species’ lifetime.

Apparently some beetles were able to track the receding margins of continental ice sheets at the end of the last glaciation. Morgan (1989) reconstructed the movements of the water scavenger beetle *Helophorus arcticus* from the last glaciation onwards. With the onset of the Wisconsin glaciation, northern Canadian populations of this beetle were forced south in eastern North America. Lowered sea level probably provided suitable habitats along the exposed continental shelf from Labrador south to New England. Inland, *Helophorus arcticus* inhabited the shores of proglacial lakes, a habitat not currently in existence at these latitudes, but one that most certainly has been available throughout much of the Quaternary history of North America. When the Laurentide ice margin retreated, *H. arcticus* populations apparently followed it back to its point of origin in arctic Canada.

Based on packrat (*Neotoma* spp.) midden fossil assemblages, the author was able to reconstruct distributional shifts for a number of species that formerly lived in the Chihuahuan Desert regions of New Mexico, Texas and the Mexican state of Coahuila (Elias, 1992). That study revealed that the various species extirpated from the Chihuahan Desert have shifted their distributions in almost every possible direction in response to changing environments.

Earlier work on postglacial shifts in the distributions of beetle species found in Rocky Mountain regional fossil assemblages (Elias, 1991) demonstrated several common patterns of range shifts in response to climate change, but since the data were collected for that paper, almost quarter of a century of new data have been generated. These new data more than triple the number of species reported to have become extirpated from the Rockies since the end of the last glaciation, bringing new patterns to light for the first time. Finally, a wealth of vertebrate fossil data from the Rocky Mountain region has now become available, with which to compare the fossil insect data.

1. **Methods**

The fossil insect assemblages discussed here comprise 122 assemblages, analysed from 13 sites, ranging from northern Montana to southern Colorado. In all cases, insect fossil remains were extracted from unconsolidated, organic-rich sediments using the kerosene flotation method described in Elias (2010). The fossil specimens recovered by this process are, for the most part, individual sclerites rather than whole exoskeletons. Beetles (Coleoptera) dominated all the assemblages, but other insect orders represented in some assemblages include ants (Hymemoptera: Formicidae), caddisfly larvae (Trichoptera) and true bugs (Hemiptera and Homoptera). Only the beetle results are reported here. Fossil identifications were based on comparison with modern museum specimens, modern specimens in the author’s collection, with the aid of taxonomic literature, and by taxonomic specialists in some families, as noted in the acknowledgements. Paleotemperature estimates made from fossil beetle assemblages follow the methods described in Atkinson et al. (1986) and Elias et al. (1996).

Regional extirpations were inferred by comparison the modern ranges of species with their fossil localities. When the fossil locality fell outside the modern range on a regional basis (i.e., the fossil locality lies in a different region than those included in the modern range), then that species was considered to have been extirpated from region of the fossil locality. The modern ranges of beetle species were taken from the literature. The modern ranges of vertebrate species were taken from the Smithsonian North American Mammals on-line database.

*2.1 Regional extirpation*

In the context of this paper, regional extirpation is defined as the absence of a species from the known modern beetle fauna of the region from which it was previously found in a fossil assemblage. In most instances, this means that a species identified from a fossil assemblage in the Rocky Mountain region is no longer found in the Rockies. In some cases, the species is known from a different part of the Rockies, but is absent from the fossil locality region. For instance, a species might inhabit the Northern Rockies today (the ranges from Alberta and British Columbia to northern Wyoming), but is absent from the Southern Rockies (the ranges from southern Wyoming to New Mexico), where it was found as a Pleistocene fossil. These are noted in the ‘Modern Range’ descriptions for species listed in Table 2.

*2.2 Data comparisons*

Thanks to the Faunmap project (Graham and Lundelius, 2010), it is now possible to compare the results of regional Quaternary insect studies with studies of contemporaneous vertebrate faunas. There are hundreds of Quaternary vertebrate faunal localities known from the Rocky Mountain region, of which ten have produced notably diverse faunal lists from the Late Pleistocene and Holocene (Table 1). Each of these sites has produced Late Pleistocene faunas of at least ten to fifteen identified species. A few, such as Bell Cave and Natural trap Cave in Wyoming and the Ziegler Reservoir site in Colorado have yielded vertebrate faunal lists including more than 20 species (see Table 3 for site references). The patterns of regional extirpation of the mammal species from the Rockies during and after the last glaciation are compared here to the patterns observed in the beetle faunas.

The other insect fossil group for which Late Pleistocene records exist for the study region is fossil Chironomidae (midges). While it might seem logical to also compare patterns of beetle and midge species extirpations, it is not yet possible to do so, for several reasons. First, almost no chironomid remains from Late Pleistocene and Holocene assemblages in western North America have been identified to the species level. Second, with the exception of the recent paper by Haskett and Porcinu (2014), very few studies of fossil midge assemblages have been done from the Rocky Mountain region. The only other published studies are from the Canadian Rockies (Walker and Mathewes, 1987, 1989; Heinrichs et al., 1999; Pellett et al, 2000; Roseberg et al., 2004), and very few of the specimens from these studies have been confidently identified to the species level.

1. **Fossil Insect Study Sites**

The kind of Late Pleistocene organic deposits that yield abundant insect fossil remains are quite rare in the Rocky Mountains, because many of the mountain ranges were glaciated during the last glaciation. The movements of glacial ice scoured high-elevation landscapes, obliterating older organic-rich sedimentary deposits. Therefore the high elevation fossil assemblages discussed here either represent postglacial times (i.e., after the ice margins retreated back upslope from the sites), or they were formed in rare high elevation localities that remained ice-free, such as the Ziegler Reservoir site near Snowmass, Colorado. A brief description of the study sites follows, in north-to-south order.

*3.1 Marias Pass, Montana*

This site is in the subalpine forest at 1,548m above sea level (asl), just south of Glacier National Park (Fig. 1). Organic lake sediments underlying Mount St. Helens Jy ash provide evidence of deglaciation by 13,400 cal yr B.P. (Carrara et al., 1986). Insect fossils extracted from this thin layer of sediment provide evidence of late glacial conditions (Elias, 1988; Elias 1996).

*3.2 False Cougar Cave, Montana*

False Cougar Cave is located in subalpine parkland, at 2,590m asl in the Pryor Mountains of southern Montana (Fig. 1). It is the first high altitude cave in this region to be excavated systematically for archaeology (Bonnichsen et al., 1986). Samples from a 11,300-year-old organic horizon within the cave have been examined for insect fossils (Elias, 1995). ). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.3 Bonneville Estates Rockshelter, Nevada*

Bonneville Estates Rockshelter is located about 50 km south of the town of West Wendover, Nevada, and is situated upon the high shoreline complex of Pleistocene Lake Bonneville (1580 m in elevation). The lake receded from its high shoreline around 17,700 cal yr BP, making the rockshelter available for both human and animal occupation (Madsen et al., 2001; Goebel et al., 2007).Bonneville Estates Rockshelter is located about 50 kmsouth of the town of West Wendover, Nevada, and issituated upon the high shoreline complex of PleistoceneLake Bonneville (1580 m in elevation). BonnevilleEstates is an open shelter that has a southeast-facingmouth reaching 10 m high and 25 m wide. From front to back, it is about 15 m deep at its deepest point. The lakereceded from its high shoreline around 14,500

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 The insect fossils were recovered from a packrat midden sample dated 13,700 cal yr BP (Elias, 2013).

*3.4 Huntington Canyon, Utah*

This site lies at 2,730m asl, south of Salt Lake City, Utah (Fig. 1). It was discovered in August, 1988, when a 1920s-vintage earthen dam began to slump due to the instability of underlying lacustrine clays. Bog and lake sediments containing a mammoth skeleton are associated with a marsh developed during a low stand of an early Holocene lake. A large sample (about 75kg) of lacustrine clayey silt from inside the mammoth skull and from surrounding sediments were found to contain substantial numbers of insect fossils (Elias, 1995). AMS radiocarbon dating of purified protein from mammoth bones yielded an age of about 13,200 cal yr B.P. (Gillette and Madsen, 1992). ). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.5 La Poudre Pass, Colorado*

A fen dammed by a late Pinedale (MIS 2) moraine at La Poudre Pass lies just below the continental divide at 3100 m altitude at the northern end of the Colorado Front Range. The site is within a few meters of tree line. Fossil insect assemblages sampled from an exposure cut at the edge of the fen span the interval from about 10,000 yr B.P. to recent (Elias, 1983; Elias et al., 1986). ). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.6 Longs Peak Inn, Colorado*

A peat bog near Longs Peak Inn (2732 m) is located just outside a glacial till that pre-dates the last glaciation in the upper montane forest near the base of Longs Peak. The peat was exposed in a ditch cut across the middle of the bog. Insect fossil assemblages spanning the interval from about 3000 yr B.P. to recent document late Holocene environments at the site (Elias et al., 1986; Elias, 1996).

*3.7 Mount Ida Bog, Colorado*

This small bog represents the highest altitude site in the study, perched at 3250 m in the alpine tundra of Rocky Mountain National Park. Late Holocene insect fossil assem­blages were extracted from a large-diameter (10 cm) core taken from the edge of the bog. The only substantial assem­blage occurred at a horizon dated 900 yr B.P. These fossils were described in Elias (1985). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.8 Roaring River, Colorado*

The Roaring River site is at a cut bank at 2800 m altitude in the upper montane forest in Rocky Mountain National Park. A 20-cm-thick organic lens dated 2400 yr B.P. yielded an extremely diverse and abundant insect fauna (Elias et al., 1986). ). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.9 Lefthand Reservoir, Colorado*

A peat bank is exposed on the northern shore of Lefthand reservoir. The fossil site lies at an elevation of 3224 m in the subalpine forest. A 1.4-m column of peat was taken from the site for insect fossil analysis (Elias, 1985). The fossil assemblages range in age from about 6,000 to 100 cal yr BP. ). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.10 Lake Isabelle, Colorado*

Lake Isabelle lies in the alpine tundra zone, 1.5 km east of the continental divide in the Indian Peaks Wilderness Area of the Colorado Front Range. Two sampling sites in the lake basin yielded Holocene insect assemblages (Elias, 1985). A deltaic deposit (3323 m altitude) yielded assem­blages from 9000 to 7800 yr old and a fen (3325 m) yielded assemblages dating from 7000 yr B.P. to recent. ). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.11 Mary Jane Ski Area, Colorado*

This site represents and ancient lake bed, situated at 2,882m asl in the subalpine forest zone of the Rocky Mountains in north-central Colorado (Fig. 1). Short and Elias (1987) investigated pollen and insect fossils from late glacial peats ranging from 17,000 to about 15,000 cal yr B.P. Paleotemperature reconstructions for the site were published in Elias (1996).

*3.12 Lamb Spring, Colorado*

Lamb Spring is located at an elevation of 1,731 m asl, 3km east of the Front Range a few kilometers south of Denver, Colorado (Fig. 1). This important Paleo­indian archaeological site contains a late glacial bone bed with possible pre-Clovis artifacts (Stanford et al., 1982). Insect fossils extracted from 30cm of the organic-rich silty clay from the bone bed horizon have yielded a rich insect fossil fauna (Elias, 1986). However, the fossil insect fauna contained a mixture of alpine tundra and prairie species. Subsequent accelerator radiocarbon dating of insect fossil specimens from the two ecological groups (Elias and Nelson, 1989; Elias and Toolin, 1990) has shown that the northern prairie fauna, dated at 21,700 cal yr B.P. is several thousand years older than the alpine tundra fauna, dated at 17,600 cal yr B.P.). ). Paleotemperature reconstructions for the site were published in Elias (1996).

*3.13 Ziegler Reservoir, Colorado*

Ziegler Reservoir is an artificially dammed lake at about 2705 m asl near the town of Snowmass Village, Colorado. The site appears to have remained unglaciated during the Pinedale glaciation, as ice flowed around the perched valley holding the lake, but did not overtop the basin. Optically stimulated luminescence (OSL) ages show that the lake sediments preserved in Ziegler Reservoir were deposited during marine isotope stages (MIS) 6, 5, and 4 (Mahan et al., 2014). During excavations for vertebrate fossils, a sequence of 26 samples were taken for fossil insect analysis (Elias, 2014). These faunal assemblages represent MIS 5e, 5c, 5b and 5a, corresponding to ages of approximately 125,000, 103,000-101,000, and 93,000 to 84,000 years BP.

*3.14 Lake Emma, Colorado*

Lake Emma is situated above treeline at 3740 m above sea level. The lake catastrophically drained into an underlying mine tunnel in 1978, allowing access to the drained lake basin for sediment sampling. Lake sediments sampled from the basin yielded insect fossil assemblages ranging in age from about 10,200-9,000 cal yr BP (Elias et al., 1991). ). Paleotemperature reconstructions for the site were published in Elias (1996).

1. **Results and Discussion**

*4.1 Trends in Rocky Mountain Insect Biogeography*

Through the last 125,000 years of insect (beetle) occupation of the Rockies, some interesting, recurrent themes of immigration have appeared. There are four principal regions of North America that are now home to beetle species that previously lived in the Rocky Mountains during the Late Quaternary: eastern North America, the boreo-arctic regions of Canada and Alaska, arctic North America, and the Pacific Northwest (PNW) region. In addition, a few species that formerly lived in the Southern Rockies are now found only in the Northern Rockies (see Figure 1 for boundaries of the three Rocky Mountain regions). Species with modern ranges confined to eastern North America are broken down into two groups: those that live throughout the eastern temperate regions, and those that are restricted to the higher mountains of the Appalachian chain, mainly in New England. The temperate climates associated with the former distribution pattern are mainly associated with warm-adapted faunas from the Rockies, such as those from the last interglacial interval. The cold climates of the latter distribution pattern are very similar to those of the boreo-arctic regions. The climates of the PNW region may reflect less extremes of winter cold and summer heat than the climates of the Southern Rockies, and the PNW climate is demonstrably wetter. The mean annual precipitation (MAP) of the Southern Rockies is about 160-300 cm (NOAA, 2014), of which about two-thirds falls as snow, whereas the MAP of the Cascade Range in Washington state ranges from about 255-380 cm (NOAA, 2013). In British Columbia, MAP is as high as 467 cm per year in some coastal sites (Environment Canada, 2013). So the MAP in the PNW region is substantially higher than that of the Southern Rocky Mountains. The boreal regions are generally cold and dry. Average temperatures of the warmest month (TMAX) range from about 13-17°C; average temperatures of the coldest month (TMIN) range from about -25 to -21°C. MAP averages about 29-45 cm in these regions (Environment Canada, 2013). TMAX in the highlands of the Southern Rockies averages about 15-17°C; TMIN averages about -8 to -5°C, and MAP averages about 160-300 cm (NOAA, 2014). So beetles with a boreal distribution reflect a much drier climate with colder winters than that of the Southern Rockies. The climate of Arctic North America is substantially colder and drier, with TMAX values from 4-10°C, TMIN values from -34 to -27°C, and MAP from 10-19 cm.

Of the 200 beetle species identified from the Rocky Mountain regional faunal assemblages, 45 species (23%) are apparently no longer resident in this region. None of the 200 species is extinct. In contrast to this, only six of 73 identified mammal species (8%) from Rocky Mountain Late Pleistocene assemblages are no longer resident in the Rockies, and 12 species on that list are now extinct. Since both groups of organisms are highly mobile, it would appear that their responses to the large-scale fluctuations of climate associated with the last 125,000 years have been considerably different.

*4.2 Range shifts during MIS 5*

All of the data discussed here for MIS 5, the sequence of climatic oscillations spanning the interval from 125,000-84,000 years BP, come from the Ziegler Reservoir site. This site is highly unusual, as it represents a high altitude lake basin, perched on a hill that remained ice-free during the subsequent glaciations of MIS 4 and 2. Apparently, ice flowed down the valleys adjacent to this hill, but never over-topped it (Miller et al., 2014). The details of beetle faunal range shifts at Ziegler Reservoir are discussed in Elias (2014). The dominant trends are as follows.

Sub-stage 5e represents the last interglacial, when seasonal temperatures at Ziegler Reservoir were as high as, or slightly higher than they are today. Several species found today only in the PNW region were identified from the MIS 5e assemblage. These include the metallic wood-boring beetle *Anthaxia prasina* and the bark beetle *Dolurgus pumilus*. *Anthaxia prasina*, in spite of being in a family normally associated with trees, is known to feed on meadow herbs, such as dandelion. *Dolurgus pumilus* is a coniferous bark beetle that attacks all species of conifers in its range. The other extirpated species from this assemblage is the rove beetle *Olophrum obtectum*. This is a riparian species found in sedges and mosses. It is widely distributed in the eastern and central United States and southeast Canada (Figure 2). While *Anthaxia prasina* made its last documented appearance in the Rockies at this time, the other three species persisted at the fossil site until the end of MIS 5.

The vertebrate faunal record from MIS 5e at Ziegler Reservoir likewise indicates summer temperatures at least as warm as today, with the presence of several coniferous forest species at the site (Sertich et al., 2014). These include the northern flying squirrel (*Glaucomys sabrinus*) and the North American river otter (*Lontra canadensis*).

 Sub-stage 5c represents a warm interval in the middle of MIS 5, but temperatures at Ziegler Reservoir were not as high as in sub-stage 5e (Elias, 2014). Extirpated species in the MIS 5c assemblages include the rove beetles *Eucnecosum brachypterum*, *Pycnoglypta lurida*, and *Lordithon longiceps*, the darkling beetle *Eleodes granulata* and the bark beetle *Hylastes nigrinus*. *Eucnecosum brachypterum* is a boreo-arctic species today. *Pycnoglypta lurida* has a modern boreo-montane distribution, with populations extending down the Appalachian chain, but not the Rocky Mountains. *Eleodes granulata* is a PNW species today, as is *Hylastes nigrinus*, although the latter species is also known from the Northern Rockies region of Idaho. *Lordithon longiceps* and *Eleodes granulata* made their last known regional appearance in sub-stage 5c, while the other species discussed here persisted at least locally until the end of MIS 5.

MIS 5b was a cold interval, with TMAX 5-6°C colder than today at Ziegler Reservoir (Elias, 2014). Extirpated species in the MIS 5b assemblages include the rove beetles *Olophrum boreale* (Paykull), *Tachinus fimbratus*, *T. schwartz*, the ant-like beetle *Sonoma margemina*, and the tetratomid beetle *Tetratoma concolor*. *Olophrum boreale* is a boreo-montane species today, with populations ranging south along the Rocky Mountains to northwest Wyoming and the Wasatch Range of Utah (Campbell, 1983). *Tachinus fimbratus* is found today in the southern boreal and temperate regions of eastern North America, from New Brunswick to Georgia in the east, and from Wisconsin to Missouri in the west (Campbell, 1973). *Tachinus schwartzi* is known only from temperate eastern North America today, with sites only as far west as Michigan. *Sonoma margemina* is found today in the PNW region, as far north as southeast Alaska. *Tetratoma concolor* lives in the boreal forest regions of Canada today.

By MIS 5b, there is a transition in the vertebrate fauna at Ziegler reservoir. Coniferous forest taxa give way to more open-ground vertebrates. Sertich et al. (2014) interpret this as a change from a woodland ecosystem to a more open, tundra ecosystem.

Sub-stage 5a saw the return of warmer temperatures at Ziegler Reservoir, with TMAX and TMIN approaching modern levels (Elias, 2014). Extirpated species in the MIS 5a assemblages include the tiger beetle *Omus audouini*, the scarab *Aegialia opaca*, and the click beetle *Agriotes apicalis*. All three species are found today only in the PNW region, possibly indicating that the climates near the end of MIS 5 were considerably moister than the modern climate of the Southern Rockies. However, the fossil specimen of *Omus* may not represent *O. audouini*, but rather an extinct linage.

 Taken as a whole, the extirpated species found in MIS 5 assemblages comprise an interesting mixture of modern distribution patterns (Figure 3). The two dominant groups, in equal proportions, are the PNW and eastern North American species. About a quarter of the extirpated species are found today in the boreo-arctic regions. These species are associated with the cold phase, MIS 5b. Finally, *Olophrum boreale* represents species that today have boreo-montane distributions that include the Northern Rockies, but no longer range as far south as the Southern Rockies. This was also found in MIS 5b assemblages, representing a colder-than-modern interval.

*4.3 Range shifts during and after the Last Glacial Maximum*

Unfortunately, no fossil insect faunas have been found in the Rocky Mountain region that date to MIS 4 or 3, the interval from approximately 75,000-25,000 years BP. As discussed above, mountain sites that pre-date the last glaciation (MIS 2, or the Pinedale Glaciation in the Southern Rockies) are extremely rare, owing to the scouring of high altitude landscapes by glacial ice.

 The Last Glacial Maximum (LGM) in the Southern Rockies is termed the Pinedale Glaciation. While radiocarbon dates from the LGM are consistently older than cosmogenic dates in this region, it appears that the LGM occurred from about 29,000-18,000 calibrated years BP (Pearce, 2004). Two sites in the Southern Rocky Mountains that date to the LGM, or immediately afterwards, are the Lamb Spring site southwest of Denver, Colorado, and the Mary Jane Ski site, in the Colorado Front Range.

As discussed above, the Lamb Spring site yielded an ecologically mixed assemblage, with species associated with the northern Great Plains found in the same assemblages as alpine tundra species. Subsequent AMS radiocarbon dating of specimens from the two ecological groups revealed that they represent two distinct ages of faunal assemblages. The older fauna, dated 21,700 cal yr BP, included the regionally extirpated species of water scavenger beetle *Helophorus splendidus*. This species is found only along the shores of the Arctic Ocean of Canada today (Figure 3). The populations that lived south of the Laurentide and Cordilleran Ice Sheets may have died out completely towards the end of the last glaciation. If that is the case, then the modern Arctic populations are derived from populations that survived the LGM in Eastern Beringia (unglaciated lowlands of Alaska and the Yukon). However, the lack of any known modern populations in the Beringian region may suggest that small populations of *H. splendidus* followed the retreating margins of the continental ice sheets as they moved northward through the last 18,000 years. This scenario has been hypothesized for the postglacial history of another member of this genus, *Helophorus arcticus* (Morgan, 1989).

The younger of the two faunas from Lamb Spring, directly dated to 17,600 cal yr BP, includes the ground beetles *Dyschirius erythrocerus* and *Dyschirius haemorrhoidalis*, the water scavenger beetle *Helophorus fenderi*, and the rove beetles *Olophrum rotundicolle*, *Tachinus elongatus* and *Gymnusa atra*. *Dyschirius erythrocerus* and *D. haemorrhoidalis* are both found today in the temperate zone of eastern North America. The former species ranges today from Newfoundland to Florida, and west to Ohio (Lindroth, 1963). The latter is found in the temperate zone of the eastern United States. *Olophrum rotundicolle* is a boreo-arctic species that ranges south along the Appalachian chain, but is not known from the Rocky Mountains today (Campbell, 1983). It was found in fossil assemblages from the Colorado Rockies that are as young as the last thousand years, but is apparently not present in the Rocky Mountain region today. *Tachinus elongatus* is a boreo-montane species, with modern populations extending south along the Rocky Mountains to the Medicine Bow Mountains of southern Wyoming (Campbell, 1973). The southern edge of its modern range is thus only about 100-200 km north of the sites from which it has been found in Colorado. It persisted in Colorado until at least 2000 years ago; its last fossil record is from the Roaring River site in Rocky Mountain National Park. In contrast to this, another rove beetle, *Gymnusa atra*, is known today only from the boreal regions of Canada and Alaska (Klimaszewski, 1979).

Several vertebrate faunas from the LGM in the Rockies include the arctic lemming, *Dicrostonyx torquatus* (see table 4). Fossil assemblages containing this cold-adapted species range in age from 39.7-14.2 ka at Porcupine Cave, Colorado (Barnosky, 2004) to 16.3 ka at Bell Cave, Wyoming (Zeimens and Walker, 1974). The presence of this arctic species is perhaps one of the strongest indicators of full-glacial conditions in the Rocky Mountains during the LGM.

The oldest faunal assemblage from the Mary Jane site is dated at 17,000 cal yr BP. This assemblage contained the rove beetle, *Olophrum boreale*. This species persisted at the Mary Jane site through the youngest assemblage, dated 15,000 cal yr BP. It was also found at the high-altitude Lake Emma site in southwestern Colorado, in an assemblage dated to 10,200 cal yr BP. This is the youngest fossil assemblage in the transect of sites that contained *O. boreale*, so presumably it was extirpated from the Rockies sometime in the early Holocene.

As shown in figure 3, about half of the extirpated species found in LGM assemblages from the study region live today in either the arctic or the boreo-arctic regions. The eastern species include the two species of ground beetles dated 17,600 yr BP, and indicative of temperate climate. Their presence in the Lamb Springs site, the lowest elevation site in the transect, may be taken as a first indication of lowland climatic amelioration following the LGM.

*4.4 Range shifts during the Late Glacial interval*

The Late Glacial interval is marked in many parts of the North Hemisphere by an initial warming period, followed by a return to glacial-style climate, then another climatic amelioration that ushered in the Holocene interglacial period. This pattern of Late Glacial oscillation has not been recorded in fossil beetle assemblages from the Rockies, although it has been seen in Late Glacial beetle sequences from the Canadian Maritime provinces (Miller and Elias, 2000) and from northern Alaska (Elias, 2001). The Late Glacial interval began about 17,000 yr BP in the Rocky Mountains, and ended about 11,600 yr BP. By that time, the margins of mountain glaciers and ice caps were retreating rapidly, exposing subalpine and then alpine landscapes for the first time in about 18,000 years. Not surprisingly, the trees of the subalpine forest did not become established at the modern treeline elevations until about 1500 years later, as soil development and primary succession had to take place before the trees could reach their elevational limits (Elias, 1985).

 The extirpated species found in Late Glacial beetle faunas from the Rockies include the ground beetle *Bembidion sulcipenne hyperboroides*, the carrion beetle *Thanatophilus trituberculatus*, the water scavenger beetles *Helophorus alternatus* LeConte, *H. sempervarians*, and *H.* *splendidus*, the rove beetles *Olophrum boreale, O. rotundicolle*, *Stenus hyperboreus*, and *Holoboreaphilus nordenskioeldi*. *Bembidion sulcipenne hyperboroides* is known today only from the boreo-arctic regions of northwest Canada and Alaska (Lindroth, 1963). It was found in the faunal assemblage from Marias Pass, Montana, dated at 13,400 cal yr BP. This locality is about 1800 km southeast of the southern limit of its known modern range in northern British Columbia. This would indicate a degree of cooling at the time of fossil deposition, which was quantified by Elias (1996) as up to 3°C cooler than modern TMAX, which is 13.9°C. The carrion beetle *Thanatophilus trituberculatus* was also found in this assemblage, and it is likewise found today only in the boreo-arctic regions of North America (Anderson and Peck, 1985). The rove beetles *Stenus hyperboreus* and *Holoboreaphilus nordenskioeldi* are both cold-adapted species. The former species is found today in the boreo-arctic regions of North America. It was part of the 15,000-year old fauna from the Mary Jane site in Colorado. *Holoboreaphilus nordenskioeldi* is an arctic species today. Its modern range includes the arctic coastal regions of North America and Siberia, as well as alpine tundra localities in Alaska and the Yukon (Campbell, 1978). This species was part of the Late Glacial assemblage from Marias Pass, Montana.

 The water scavenger beetles listed above have very different modern distributions. *Helophorus alternatus* is found today only in California and Oregon (Smetana, 1985). This species was found in Mary Jane site assemblages ranging from 16,000-15,000 cal yr BP. On the other hand, *Helophorus sempervarians* is a boreo-arctic species today, with no known populations in the western United States (Figure 2). This species has only been found in a 15,000-year old assemblage from Mary Jane. Finally, *Helophorus splendidus* is an arctic species, as discussed above. Its youngest occurrence in Rocky Mountain fossil assemblages also comes from the 15,000-year old assemblage at Mary Jane. The climatic regimes associated with the modern populations of the three co-occurring species of *Helophorus* from the Late Glacial assemblages at the Mary Jane site seem incompatible, and there is certainly no one region where all three species co-occur today. This is the so-called ‘no modern analogue’ scenario of fossil assemblages that is so typical of the Late Glacial interval. This was a period of rapid environmental change when the members of biological communities in the temperate and northern latitudes were changing rapidly. The general consensus is that glacial-interglacial transitions foster climatic conditions not seen during more stable glacial and interglacial periods, and that these transitional climates have no modern counterpart. Disharmonious plant communities occur under such circumstances (Williams and Jackson, 2007), as well as disharmonious vertebrate faunas (FAUNMAP Working Group, 1996). This may well be the explanation for the no-modern-analogue beetle assemblages of this transitional interval, but it should also be kept in mind that the fossil beetle assemblages discussed here each represent up to 500 years of fossil accumulation. Thus it should not be surprising that the associations of species in such assemblages appear to be climatically discordant, especially given the rapidity and magnitude of environmental change during the Late Glacial interval. They may very well represent several stages of insect faunal change in response to rapidly changing climates.

 The mix of modern ranges seen in the Late Glacial faunas from the Rockies is dominated by cold-adapted species found today in the arctic and boreo-arctic regions (Figure 3). About a quarter of the species are found today in the PNW region, with the remainder being found today either in eastern North America or in the Northern Rockies. The PNW and eastern modern ranges of some extirpated species show that climatic amelioration was also a feature of regional climates during this interval. Interestingly, while the migration corridors between the Rockies and the PNW region remained open for beetles after the Late Glacial interval, migration between eastern North America and the Rockies appears to have stopped in the early Holocene, about 11,000 years ago.

 One other Late Glacial beetle assemblage is included in Table 2, the Bonneville Estates site from the Utah-Nevada border. This was done to highlight an interesting set of zoogeographic histories for species that lived in a formerly wet region that has now become extremely arid. As discussed in Elias (2013), the fossil beetle evidence indicates that environments of the Great Basin during MIS 2 had MAP 2-3 times that of today, and temperatures depressed by 5-6°C. This substantially cooler, wetter climate supported a very different beetle fauna from the species found there today. The Bonneville Estates fossil assemblage has been dated from 14,000 cal yr BP (Goebel et al., 2007). The species from this assemblage are indicated by an asterisk in Table 2. Three species of darkling beetles were identified from this assemblage that have subsequently been extirpated from the region: *Eleodes cuneaticollis*, *E. dentipes*, and *E. tenebrosa*. *Eleodes cuneatocillis* and *E.* dentipes are found today only in the coastal regions of California (Blaisdell, 1909). *Eleodes tenebrosa* is restricted today to the Sierra Nevada Mountains. Several species of ground beetles from the Bonneville Estates assemblage have also been regionally extirpated. *Pterostichus castaneus* and *Amara californica* are both found today in the PNW region, as is *Harpalus fraternus*, although the latter species ranges east to the southern part of the Canadian Rockies (Lindroth, 1966). Another ground beetle, *Amara ellipsis*, is found today throughout the temperate and boreal regions of North America, but not in any desert regions.

*4.5 Range shifts during the Early Holocene*

The early Holocene was the time of maximum warming of the current interglacial. Temperature reconstructions based on fossil beetle assemblages in the Rockies indicate that TMAX values peaked about 11,500 years ago, reaching levels as warm or slightly warmer than today. Both summer and winter temperatures had begun cooling by about 10,000 years ago (Elias, 1996). For the sake of simplicity, the early Holocene interval is taken here to mean 11,500-5,000 years ago. The extirpated species found in early Holocene beetle faunas from the Rockies include the ground beetles *Bembidion rusticum lenensoides* and *B. sierricola*, the rove beetles *Phlaeopterus longipalpus* and *Stenus dissentiens*, *S. sibiricus* and *S. vexatus*, the scarab *Dialytes ulkei*, and the bark beetle *Phloeotribus piceae*. *Bembidion rusticum lenensoides* is found today in the western boreo-arctic region, much like *B. sulcipenne hyperboroides*. It was found in a fossil assemblage dated 9000 cal yr BP at Lake Emma, Colorado. *Bembidion sierricola* is known today only from the mountain ranges of the Pacific coast. Its last appearance in Rocky Mountain fossil assemblages was also at 9000 cal years BP at Lake Emma. Unfortunately, no fossil beetle research has been carried out in any California highlands, so we know nothing of the beetle faunal history of this region.

 The rove beetle *Phlaeopterus longipalpus* is an alpine snowfield species, known today from the high mountains of the PNW region, extending southeast to Utah (Hatch, 1957). It was found in fossil assemblages from the high altitude site of La Poudre Pass, Colorado, in assemblages ranging from 10,000-1500 cal yr BP. Thus it would seem that its extirpation from the Southern Rockies has been quite recent. The four species of the rove beetle genus *Stenus* discussed above have widely varied modern distributions. *Stenus dissentiens* is known today from the northern tier of states, including Michigan, Idaho and Washington, in addition to southern British Columbia (Hatch, 1957). *S. vexatus* is known from the Canadian provinces of British Columbia, Alberta, and Manitoba. *S. sibiricus* is known only from the Arctic (Campbell and Davies, 1991). *Stenus dissentiens* and *S.* vexatus were both found in a number of Holocene-age assemblages, ending with late Holocene assemblages less than a thousand years old. *Stenus sibiricus* was found in a sequence of assemblages ranging from 11,000-9000 years old from Lake Isabelle, Colorado.

 The scarab beetle *Dialytes ulkei* is an eastern North American species today. A deer-dung feeder, it ranges from the boreal through the temperate zones (Gordon and Skelley, 2007). It was found in an 11,000-year old fossil assemblage from La Poudre Pass; this is the youngest fossil assemblage from the Rockies that included any species restricted today to eastern North America. The bark beetle *Phloeotribus piceae* attacks all species of conifers in its range, which includes the boreal and temperate regions of North America. Unlike some other generalist coniferous bark beetles, this species does not range south along the coniferous forests of the Rockies. Its most recent appearance in the regional fossil record is from 6000 years ago at la Poudre Pass, Colorado.

 The overall composition of early Holocene species subsequently extirpated from the Rockies is an even split between taxa currently found in the PNW region, and those found in the boreo-arctic regions (Figure 3). As mentioned above, the last species with a modern range restricted to eastern North America was last seen from the Rocky Mountain fossil record of 11,000 years ago. Migration corridors have almost certainly existed between the Rockies and both the PNW and boreal regions. By migrating along the Rocky Mountain chain, species could find suitable environmental conditions along the way to either region. However, with the arrival of interglacial conditions on the Great Plains, that migration corridor was blocked for species requiring cool to cold summer climates with medium levels of moisture.

*4.6 Range shifts during the Late Holocene*

The latter half of the Holocene saw climatic cooling in the Rocky Mountain region, especially in the last 3000 years, when both summer and winter temperature averages dropped below modern levels (Elias, 1996). The extirpation of seven species has been documented for the region, including the ground beetle *Bembidion striola*, the rove beetles *Olophrum rotundicolle*, *Tachinus elongatus*, *Oxytelus montanus*, *Gymnusa atra*, and *Stenus vexatus*, and the bark beetle *Scierus pubescens*. *Bembidion striola* is confined today to the Pacific coastal mountain ranges (Lindroth, 1963). Its last known occurrence in the Rockies was at 2000 cal years BP at the Roaring River site, Colorado. The last known occurrence of *Oxytelus montanus* was at 2000 cal years BP at the Longs Peak Inn bog site. This species is found today in the PNW region, with an outlying population in the Cypress Hills of Saskatchewan (Hatch, 1957; Hooper and Larsen, 2013). Finally, the bark beetle *Scierus pubescens* is known today from the PNW region, extending east to northern Montana. This beetle attacks spruce, subalpine fir, and various species of pine (Bright, 1976).

 Taken together, most of the late Holocene species extirpated from the Rockies are now found in the PNW (Figure 3). The other important modern distribution pattern for these species is the boreo-arctic regions of Canada and Alaska. Perhaps the most surprising aspect of the late Holocene faunas is that so many species were extirpated so recently from the Rockies. Of the 45 species known to have been extirpated from this region in the last 125,000 years, eight died out regionally within the last few thousand years. This speaks to the dynamism of insect migration. Each species is constantly attempting to become established in new regions. There are no stable insect communities, in any meaningful sense of the term. According to Coope (1970), this constant shifting of ranges rarely allows for genetic isolation of populations for sufficient lengths of time for speciation to occur, hence the somewhat unexpected situation wherein short-lived organisms have neither evolved many new species nor suffered appreciable numbers of extinctions throughout the Quaternary. This is in sharp contrast to the mammals, in which significant numbers of species have evolved, and large numbers have become extinct during this interval.

*4.7 Trends in Rocky Mountain Mammal Biogeography*

A survey of ten prominent vertebrate fossil sites in the Rocky Mountains with Late Pleistocene and Holocene-age faunas (Table 3) produced a combined list of 62 identified species: less than a third of the number of identified beetle species from this region and time interval. However, the starkest contrast between the beetle and mammal species lists is that 12 out of the 73 mammal species are now extinct (16% of the fauna). These include *Arctodus simus*, *Bison latifrons*, *Bootherium bombifrons*, *Canis dirus*, *Equus conversidens*, *Homotherium serum*, *Mammut americanum*, *Mammuthus columbi*, *Megalonyx jeffersoni*, *Microtus meadensis*, *Miracinonyx trumani*, and *Panthera atrox*.

Of the 72 species identified from these Late Pleistocene faunal assemblages, only six of the extant species have been extirpated from the Rocky Mountain region (Table 4). The most recent fossil record of the eastern spotted skunk, *Spilogale putorius*, was during the late glacial interval Haystack Cave in southern Colorado (Emslie, 1986). The nearest modern populations of this skunk are on the Great Plains of eastern Colorado. Although this species lives in the central and southern Appalachian Mountains, its modern range does not include any part of the Rocky Mountains (http://www.iucnredlist.org/, accessed April 2014).

The pygmy rabbit, *Brachylagus idahoensis* was found in Late Pleistocene faunal assemblages (not radiometrically dated) from Porcupine Cave, central Colorado. Today this species inhabits almost the entire Great Basin region, with its easternmost populations in the western foothills of the Wasatch Mountains of Utah (http://www.iucnredlist.org/, accessed April 2014). The range of this species is tied closely to that of big sagebrush (*Artemisia tridentata*), which is the primary food source of the species.

Collared lemming fossils were identified from three Late Pleistocene faunal assemblages from Wyoming, including Little Canyon Creek Cave (Walker, 1987), Natural Trap Cave (Gilbert and Martin, 1984), and Bell Cave (Zeimens and Walker, 1974). They were also reported from Late Pleistocene assemblages from January Cave in southern Alberta, Canada (Burns, 1991). The youngest appearance of collared lemming in the Rockies was 14,200 cal yr BP, at Little Canyon Creek Cave. Apparently it inhabited at least the Northern Rockies during the last glaciation. Assignment of collared lemming fossil specimens to the species level is quite difficult. As discussed in Fulton et al. (2013), most collared lemming fossils from sites in the Rocky Mountains were identified as the Palearctic collared lemming, *Dicrostonyx torquatus,* based on assumptions held at the time about that species’ ecological requirements and modern range. At one time this species was thought to include most or all New World lemmings, but genetic evidence indicates that *D. torquatus* is strictly Eurasian (Wilson and Reeder, 2005). Today this species is found in arctic and subarctic regions of Siberia. This lemming inhabits arctic and subarctic tundra and forest-tundra with dwarf willow (Salix spp.) shrubs (http://www.iucnredlist.org/ accessed April 2014). However, Fulton et al. (2013) analysed ancient DNA from fossil *Dicrostonyx* specimens found in assemblages from the last glaciation in Iowa and South Dakota, and they concluded that the lemmings that survived the last glaciation south of the Laurentide Ice Sheet in North America were actually Richardson’s collared lemming (*D. richardsoni*), a species found today in both arctic tundra and boreal forest regions of Canada east of Great Slave Lake and west of Hudson Bay. The ancient DNA research supports the hypothesis that *D. richardsoni* was the collared lemming found in the Rocky Mountain region fossil assemblages from the last glaciation. It may have followed the retreating margins of the Laurentide and Cordilleran Ice Sheets into Canada at the end of the last glaciation.

The mountain hare, *Lepidus timidus* is found today only in the boreo-arctic regions of Eurasia. It is not known from North America. Fossil specimens of this species were identified from Natural Trap Cave, Wyoming (Gilbert and Martin, 1984), in assemblages ranging in age from 24,500 to 15,300 cal yr BP. Since this is a conspicuous mammal, it seems highly unlikely that any modern populations in North America would have gone undetected by mammalogists.

The southern bog lemming, *Synaptomys cooperi* lives today in eastern North America, extending west to Kansas, south to Tennessee and Arkansas, and north to southern Ontario and Quebec (Wilson and Choate, 1997). Fossil remains of this lemming were identified from Ziegler Reservoir, Colorado, in an assemblage dated to MIS 6 (ca. 140,000-130,000 yr BP) (Graham et al., 2014). The fossil flora and fauna associated with this interval at Ziegler Reservoir are indicative of the final stages of the Bull Lake glaciation – the most extensive Late Pleistocene glaciation in the Rockies (Miller et al., 2014). Based on the Faunmap records (Graham et al., 2010), this lemming has not been found in any other Quaternary vertebrate fossil assemblage from the Rocky Mountain region.

In summary, of the six mammal species that have been extirpated from the Rocky Mountains since the last glaciation, two are now found to the east, on the Great Plains and beyond, one is now found to the west, in the Great Basin, two are now found to the north, in the boreal regions, and one is now found far to the north, in the Arctic. Unlike the beetles, there are no mammals in the Rocky Mountain Late Pleistocene fossil record that are found exclusively today in the Pacific Northwest region. The PNW does have a distinctive modern mammalian fauna, including several species found nowhere else (Table 5). Of these 14 PNW species, five have fossil records restricted to the PNW region, two have been found in Late Pleistocene tar pit deposits in southern California, five have no fossil record documented in Faunmap, and only one, Keen’s Myotis (*Myotis keenii*) has a fossil record well outside the PNW region, in the eastern and central United States. More to the point, none of these PNW species have been found in any Rocky Mountain fossil assemblages. Based on these data, it appears that there has been little or no mammalian faunal exchange between the PNW region and the Rocky Mountains during the Pleistocene or Holocene. This is in stark contrast to the fossil beetle record, where PNW species are a substantial component in all but LGM-age faunas, right through to the late Holocene. With the exception of the mountain beaver, all the species listed in Table 5 are small mammals. It could be argued that the two species of moles may not be able to disperse rapidly into new regions, but the squirrels, voles, chipmunks, shrews and deer mouse should have been able to move back and forth between the PNW region to the Northern Rockies, and from there spread south along the mountain chain.

This discrepancy between the zoogeographic histories of insects and mammals leaves us with a conundrum. It could be argued that a few of the PNW beetle species found in Rocky Mountain fossil assemblages were living in cool, wet microhabitats, but it strains credulity to consider that more than twenty species from nine different families of beetles could all have been associated with such a microhabitat, especially since these species include predators, scavengers, dung beetles, herbaceous plant feeders and coniferous bark beetles. The beetle record, then, clearly indicates that there was an insect migration corridor between the Rocky Mountains and the PNW that remained open for much of the Late Pleistocene, and persisted until the last millennium. Why did no mammals make use of this corridor? Were there barriers to mammal migration that were surmounted by insects? Was it the r-selected reproductive strategy of insects (having hundreds or thousands of offspring, most of which attempt to migrate into new regions) that gave them this ability to exploit new territories with suitable environments? Small mammals reproduce rapidly and are usually good dispersers. Why did they not show the same patterns of dispersal out of the PNW region as the insects? These remain open questions.

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Table 1. Late Quaternary insect fossil localities in the Rocky Mountain region

|  |  |  |  |
| --- | --- | --- | --- |
| Site | Abbreviation in Fig. 1, Table 1 | Age range of faunas (calibrated yr BP X 1000) | Reference(s) |
| Bonneville Estates, NV | BE | 13.7 ka | Goebel et al., 2007; Elias, 2013 |
| False Cougar Cave, MT | FCC | 11.3 ka | Elias, 1995 |
| Huntington Canyon, UT | HC | 10.7 ka | Elias, 1995 |
| Lamb Spring, CO | LS | 21.7 ka, 17.6 ka | Elias, 1986; Elias and Nelson, 1989; Elias and Toolin, 1990 |
| Lake Emma, CO | LE | 10.2-8.9 ka | Elias et al., 1991 |
| Lake Isabelle, CO | LI | 11.5-9 ka | Elias, 1985 |
| La Poudre Pass, CO | LPP | 11.3-0.1 ka | Elias, 1983; Elias et al., 1986 |
| Lefthand Reservoir, CO | LR | 6.2-0.1 ka | Elias, 1985 |
| Longs Peak Inn Bog | LPB | 3.2-0.2 | Elias et al., 1986; Elias, 1996 |
| Marias Pass, MT | MP | 13.4 ka | Elias, 1988, 1996 |
| Mary Jane Ski Area, CO | MJ | 16.8-14.6 ka | Short and Elias, 1987; Elias, 1996 |
| Mount Ida Bog Pond, CO | MIP | 10.2-5.3 ka | Elias, 1985, 1996 |
| Roaring River, CO | RR | 2.5 | Elias, et al., 1986 |
| Ziegler Reservoir | ZR | 125-77 ka | Elias, 2014 |

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| Table 2. Species no longer present in the Central and Southern Rocky Mountains, showing their modern ranges and age of fossil occurrences in the Rockies |
|  |
|  |  | Sites and Age Range |
| Species | Modern range | ZR | LS | MJ | BE | MP | HC | LPP | LI | FCC | LE | MIP | RR | LR | LPB |
| CICINDELIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Omus audouini* Reiche | PNW | 5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| CARABIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Dyschirius erythrocerus* LeC | E North America |  | 17.6 |  |  |  |  |  |  |  |  |  |  |  |  |
| *Dyschirius haemorrhoidalis Dej*. | E North America |  | 17.6 |  |  |  |  |  |  |  |  |  |  |  |  |
| *Bembidion rusticum lenensoides* Lth. | W Boreo-arctic |  |  |  |  |  |  |  |  |  | 9 |  |  |  |  |
| *Bembidion sierricola* Csy. | Pacific coast ranges |  |  |  |  |  |  |  |  |  | 10-9 |  |  |  |  |
| *Bembidion striola* LeC. | Pacific coast ranges |  |  |  |  |  |  |  |  |  |  |  | 2 |  |  |
| *Bembidion sulcipenne hyperboroides* Lth. | W Boreo-arctic |  |  |  |  | 13.4 |  |  |  |  |  |  |  |  |  |
| *Pterostichus castaneus* Dej.  | PNW |  |  |  | 14 |  |  |  |  |  |  |  |  |  |  |
| *Amara californica* Dej.  | PNW |  |  |  | 14 |  |  |  |  |  |  |  |  |  |  |
| *Amara ellipsis* Csy.  | Temperate & Boreal |  |  |  | 14 |  |  |  |  |  |  |  |  |  |  |
| *Harpalus fraternus* LeC.  | PNW, Canadian Rockies |  |  |  | 14 |  |  |  |  |  |  |  |  |  |  |
| HELOPHORIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Helophorus alternatus* LeC. | CA and OR |  |  | 16-15 |  |  |  |  |  |  |  |  |  |  |  |
| *Helophorus fenderi* McCork. | WA and OR |  | 17.6 |  |  |  |  |  |  |  |  |  |  |  |  |
| *Helophorus sempervarians* Ang. | Boreo-arctic |  |  | 15 |  |  |  | 4-2 |  |  |  |  |  |  |  |
| *Helophorus splendidus* Ang. | Arctic |  | 21.7 | 15 |  |  |  |  |  |  |  |  |  |  |  |
| SILPHIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Thanatophilus trituberculatus* Kby. | Boreo-arctic |  |  |  |  | 13.4 |  |  |  |  |  |  |  |  |  |
| STAPHYLINIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Eucnecosum brachypterum* (Grav.) | Boreo-arctic | 5c,5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Phlaeopterus longipalpus* Csy. | PNW southeast to UT |  |  |  |  |  |  | 10-1.5 |  |  |  |  |  |  |  |
| *Olophrum boreale* (Payk.) | Boreomontane to WY | 5b/5a |  | 17-15 |  |  |  |  |  |  | 10.2 |  |  |  |  |
| *Olophrum obtectum* Er. | E North America | 5e,5b/5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Olophrum rotundicolle* Salhb. | Boreo-arctic + Appalachia |  | 17.6 | 16-15 |  |  |  | 10-0.1 | 11-9 |  |  | 10-5 | 2 | 6-0.1 | 3-0.4 |
| *Holoboreaphilus nordenskioeldi* (Mäkl.) | Arctic-Alpine Canada, AK |  |  |  |  | 13.4 |  |  |  |  |  |  |  |  |  |
| *Pycnoglypta lurida* (Gyll.) | Boreo-montane, not Rockies | 5c,5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Tachinus contortus* Hatch | PNW, MT |  |  |  |  |  |  |  | 11-9 |  |  |  |  |  |  |
| *Tachinus elongatus* Gyll. | Boreo-montane, to WY |  | 17.6 |  |  |  |  |  | 11-9 |  |  |  | 2 |  |  |
| *Tachinus fimbratus* Grav. | E North America | 5b |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Tachinus schwartzi* Horn | E North America | 5b/5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Lordithon longiceps* LeC. | Boreal Canada, AK | 5c |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Oxytelus laqueatus* (Marsh.) | Boreal Canada, AK | 5e-5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Oxytelus montanus* Csy. | PNW, Cypress Hills, Sask. |  |  |  |  |  |  | 10.5 |  |  |  |  |  |  | 3-2 |
| *Gymnusa atra* Csy. | Boreal Canada, AK |  | 17.6 |  |  |  |  |  |  |  |  |  |  |  | 3-0.2 |
| *Stenus dissentiens* Csy. | MI, WA, OR, ID, BC |  |  |  |  |  |  | 2-0.1 | 11-9 |  |  | 10-5 |  |  |  |
| *Stenus hyperboreus* Sahlb. | Boreo-arctic |  |  | 15 |  |  |  |  |  |  |  |  |  |  |  |
| Table 2, continued |  |  |
|  |  |  |
|  |  | Sites and Age Range |
| Species | Modern range | ZR | LS | MJ | BE | MP | HC | LPP | LI | FCC | LE | MIP | RR | LR | LPB |
| *Stenus sibiricus* Sahlb. | Arctic |  |  |  |  |  |  |  | 11-9 |  |  |  |  |  |  |
| *Stenus vexatus* Csy. | BC, Alta, Man |  |  |  |  |  |  |  |  |  |  |  |  | 6-0.1 |  |
| PSELAPHIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Sonoma margemina* Park & Wag. | PNW to Southeast AK | 5b,5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| SCARABAEIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Aphodius malkani* Hatch | ID |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Aegialia cylindrica* Eschz. | PNW to Southeast AK |  |  |  |  |  | 13.2 |  |  | 11.3 |  |  |  |  |  |
| *Aegialia opaca* Brown | PNW | 5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Dialytes ulkei* Horn | E North America |  |  |  |  |  |  | 11 |  |  |  |  |  |  |  |
| ELATERIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Agriotes apicalis* LeC. | PNW | 5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| TENEBRIONIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Eleodes cuneaticollis* Csy. | Coastal N CA |  |  |  | 14 |  |  |  |  |  |  |  |  |  |  |
| *Eleodes dentipes* Esch.  | Coastal CA |  |  |  | 14 |  |  |  |  |  |  |  |  |  |  |
| *Eleodes granulata* LeC. | PNW | 5c |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Eleodes tenebrosa* Fall  | Sierra Nevada of CA |  |  |  | 14 |  |  |  |  |  |  |  |  |  |  |
| TETRATOMIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Tetratoma concolor* LeC. | Boreal Canada | 5b |  |  |  |  |  |  |  |  |  |  |  |  |  |
| BUPRESTIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Anthaxia prasina* Horn | PNW | 5e |  |  |  |  |  |  |  |  |  |  |  |  |  |
| SCOLYTIDAE |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Dolurgus pumilus* Eich | PNW to Southeast AK | 5e,5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Scierus pubescens* Sw. | PNW, MT |  |  |  |  |  |  |  |  |  |  |  |  | 6-0.1 |  |
| *Hylastes nigrinus* (Mannh.) | PNW, N Rockies to ID | 5c, 5b, 5a |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *Phloeotribus piceae* Sw. | Eastern N America, PNW |  |  |  |  |  |  | 11.5-6 |  |  |  |  |  |  |  |

Table 3. Late Pleistocene and Holocene fossil vertebrate sites in the Rocky Mountain region

|  |  |  |  |
| --- | --- | --- | --- |
| Site | Abbreviation in Fig. 1 | Age range of assemblages (cal yr BP X 1000) | Reference |
| Bell Cave, WY | BC | 16.3-11.7 ka | Zeimens and Walker, 1974 |
| Chimney Rock Animal Trap, CO | CR | 13.9-2.6 ka | Hager, 1972 |
| Colby mammoth site, WY | CM | 13.1-12.9 ka | Frison and Todd, 1986 |
| Haystack Cave, CO | HSC | 18.2-14.9 ka | Emslie, 1986 |
| January Cave, ALTA | JC | 39.6-27.3 | Burns, 1991 |
| Little Canyon Creek Cave, WY | LCC | 39.7-14.2 ka | Walker, 1987 |
| Merrell, MT | MR | 29.3 ka | Dundas et al., 1996 |
| Natural Trap Cave, WY | NT | 24.5-1 ka | Gilbert and Martin, 1984 |
| Porcupine Cave, CO | PC | Late Pleistocene | Barnosky, 2004 |
| Ziegler Reservoir, CO | ZR | MIS 5-4 | Graham et al., 2014 |

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| --- |
| Table 4. Extralimital mammal species from Late Pleistocene fossil assemblages in the Rocky Mountains |
|  |  |  |  |  |
| Species | Locality | Age of assemblage (calibrated yr BP X 1000) | Modern range | Reference |
| *Glaucomys sabrinus* Shaw*Lontra canadensis* Shreber*Urocitellus elegans* Kennicott*Synaptomys cooperi* Baird | Ziegler Reservoir, COZiegler Reservoir, COZiegler Reservoir, COZiegler Reservoir, CO | MIS 5e, 5dMIS 5eMIS 5MIS 6 | Boreal, PNWBoreal, PW, EasternWyoming, Idaho, MontanaEastern, central North America | Sertich et al., 2014Sertich et al., 2014Sertich et al., 2014Sertich et al., 2014 |
| *Spilogale putorius* (L.) | Haystack Cave, CO | 18.2-14.9 k | Great Plains | Emslie, 1986 |
| *Brachylagus idahoensis* (Merriam) | Porcupine Cave, CO | Late Pleistocene | Great Basin | Barnosky, 2004 |
| *Dicrostonyx torquatus* (Pallas)*Dicrostonyx torquatus* (Pallas) | Little Canyon Creek Cave, WYJanuary Cave, Alta | 39.7-14.2 k37.4-27.6 k | ArcticArctic | Walker, 1987Burns, 1991 |
| *Dicrostonyx torquatus* (Pallas) | Natural Trap Cave, WY | 24.5-15.3 k | Arctic  | Gilbert & Martin, 1984 |
| *Dicrostonyx torquatus* (Pallas) | Bell Cave, WY | 16.3 | Arctic | Zeimens & Walker, 1974 |

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| Table 5. Fossil records of mammal species restricted today to the Pacific Northwest region  |
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| Species | Common name | Fossil record and age range of finds |
| *Aplodontia rufa* (Rafinesque) | Mountain beaver | Mostly PNW, one in Nevada (4700-1200 ka) |
| *Tamiasciurus douglasii* (Bachman) | Douglas’s squirrel | PNW region only (20-1 ka) |
| *Callospermophilus saturatus* (Say) | Cascade golden-mantled ground squirrel | None |
| *Zapus trinotatus* Rhoads | Pacific jumping mouse | None |
| *Tamias townsendii* (Bachman) | Townsend’s chipmunk | PNW region only (3-0.1 ka) |
| *Microtus oregoni* (Bachman) | Creeping vole | None |
| *Microtus townsendii* (Bachman) | Triangle Island vole | PNW region only (10-0.2 ka) |
| *Peromyscus keeni* (Rhoades) | Northwestern deer mouse | None |
| *Sorex bendirii* (Merriam) | Pacific water shrew | McKittrick, California (40-10 ka) |
| *Sorex trowbridgii* (Baird) | Trowbridge’s shrew | Carpinteria, California (40-10 ka) |
| *Scapanus orarius* (True) | Coast mole | PNW region only (12-0.2 ka) |
| *Scapanus townsendii* (Bachman) | Townsend’s mole | PNW region only (0.4-0.1 ka) |
| *Neurotrichus gibbsii* (Baird) | Shrew-mole | None |
| *Myotis keenii* (Merriam) | Keen’s Myotis (bat) | Eastern and central United States (110-3 ka) |



Figure 1. Map of the Rocky Mountain region, showing locations of fossil insect sites (circles) and fossil vertebrate sites (triangles) discussed in text. Shaded areas represent mountainous regions.



Figure 2. Modern distribution maps for species discussed in text. Map for *Olophrum obtectum* from Campbell, 1983. Map for *Dolurgus pumilus* from Bright, 1976. Map for *Helophorus splendidus* and *H. sempervarians* from Smetana, 1985.



Figure 3. Percentage composition of species found in various intervals of the Late Pleistocene, based on their modern distributions.