2004

Beyond Ecology: Bugs Reveal the Deep Roots of Grassland Ecoregions

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Abstract

Northern grassland faunas that were most affected by glaciation-induced climate shifts include more than 225 endemic phytophagous bugs (leafhoppers and related insects, the Homoptera-Auchenorrhyncha) on Canadian plains, and another 275 in Pacific Northwest intermontane grasslands. These exceptionally rich endemic faunas include many insect-plant associations common to related species of bugs, suggesting adaptation to certain environmental factors that persisted over millions of years despite radical environmental changes induced by glacial advances and retreats. Smaller, but significant, endemic faunas of Homoptera-Auchenorrhyncha in other glaciated areas also reveal patterns of ancient ecological areas. Groups of these grassland-endemic bugs are common to grassland areas, which are equivalent to "ecoregions." Significant differences between these bug-defined areas and currently defined ecoregions suggest that our present definitions are insufficiently accurate for establishing conservation priorities.

Keywords: biogeography, palaeo-ecology, ecoregions, leafhoppers, planthoppers

Introduction

Community structure (the interactions of modern biota) is usually assumed to be the basis on which ecosystems are defined and conservation priorities are established (NatureServe 2004). Yet modern ecological characteristics of native prairies, such as plant dominance and trophic webs, are highly localized and geologically fleeting phenomena, particularly in temperate and northern regions. Community ecology can represent only the situation extant during the most recent 10,000 years or less. This results in conservation priorities designed to restore a stability that never existed because ecosystems have been in flux for millennia. Moreover, ecosystems will probably continue to change as global warming becomes more pervasive (Whitlock 1992). What conservation priorities need is a long-term definition of an ecosystem that builds upon the most stable elements in the environment. This, in turn, requires a basis in palaeo-ecology.

Palaeo-ecology is an attempt to provide a broader perspective to ecology based on inferences from a variety of data sources. Studies of ice cores from permanent glaciers and diatoms from ocean floor samples give evidence of widespread climate fluctuations over the millennia, while more localized phenomena, such as floristic communities, can be studied from microfossils and pollen in lake sediments. Using this evidence, climatologists have shown that glacial episodes have been punctuated by a series of isolated interglacial periods and shorter, more localized interstadial periods. None of these warm periods are known to have lasted more than 50,000 years and most were shorter than 10,000 years (Williams 1998). All were embedded in a pervasive glacial era (the Pleistocene) spanning at least a million years. Throughout the Pleistocene, plant communities constantly shifted and probably recombined as world temperatures rose and fell.

The extent of grasslands in particular seems to have fluctuated greatly during the Pleistocene. Unfortunately, no palynological data differentiates types of grasslands because pollen grains of *Artemisia* and grasses are evidence only of grasslands in general, but cannot be used to identify the species of plants that are characteristic of different grassland ecosystems. Subfossils of ground beetles are favored in such studies because these insect remains are identifiable to species, and these species are known to rapidly follow environmental gradients (Bennett 1997). Unfortunately, such subfossils are best preserved in permafrost and, therefore, are limited to northern regions. One must find other data to discover the deep roots of modern temperate-zone grassland ecosystems.

Endemism is one way to infer long-term ecosystem stability. Organisms that are endemic to a particular ecosystem appear to be limited in their distribution by very specific ecological requirements or by geographic barriers to dispersal. In grasslands, endemism is largely defined by localized plants (Ricketts and others 1999) since most prairie vertebrates and showy invertebrates (such as butterflies) tend to occupy large ranges or are migratory. Little attention has been paid to other invertebrate groups that are speciose and endemic to prairies. This study examines grassland-endemic Homoptera-Auchenorrhyncha or "short-horned bugs" (Figure 1) for evidence of grassland paleo-ecology. These insects are utilized seldom in ecological studies, although they include hundreds of grassland endemics in Canada and the northern United States (Hamilton 2002, 2004*a*).

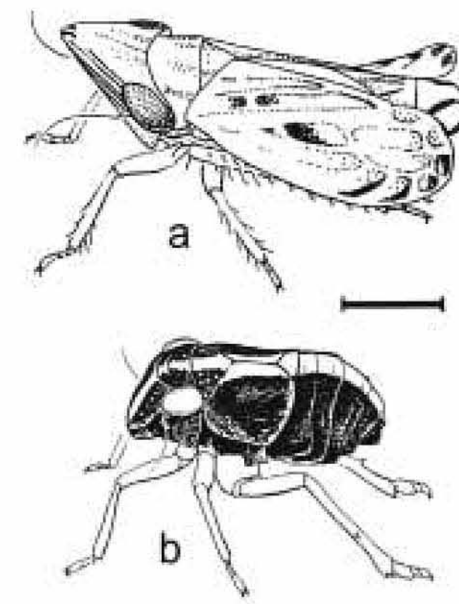

Figure 1. Flightless Homoptera-Auchenorrhyncha. (a) a leafhopper, *Flexamia*, with aborted hind wings; (b) a planthopper, *Bruchomorpha*, with wings reduced to scales, exposing the abdomen. Scale line: 1 mm.

Short-horned bugs include planthoppers (Fulgoroidea), spittlebugs (Cercopoidea), cicadas (Cicadoidea), and treehoppers (Membracidae) but the majority are leafhoppers (Cicadellidae). Leafhoppers include more than 800 species characteristic of the Great Plains (Oman 1949). These grassland insects maintained a very close association with their hosts while evolving in grassland situations (Ross 1970). Leafhoppers are at once common, diverse, localized, and easily collected in prairie remnants (Hamilton 1995). Many grassland-endemic leafhopper species are oligophagous and have a very limited range of host plants, usually a small group of related species (Nickel 2003). Others are monophagous, with only one host species that is a dominant or subdominant perennial in particular native grassland ecosystems (Whitcomb and others 1994). This close association of common plant and insect seems to be the main reason why so many leafhoppers are endemic to grasslands.

Leafhoppers and related insects include many prairie-endemic species that reflect broad ecological zones (Hamilton 2004*a*). How these insects can be used in ecological studies is currently under investigation. Preliminary analyses suggest that leafhopper distributions accurately map "ecoregions" defined by dominant vegetation and are particularly valuable as indicators of ecosystems when very little native grassland remains (Hamilton 2005). The short-horned bug fauna is rich enough that significant differences in their distributions from those of other prairie endemics could alter our whole understanding of ecoregions, thus impacting conservation priorities. This report summarizes what we now know and can surmise about the value of leafhoppers and related insects to our understanding of ecoregions.

Observations

Preliminary analysis of short-horned bugs in Canada shows a very poor fit between the distribution of endemic bugs (Hamilton 2004*b*) and currently defined prairie ecoregions—areas that are classified mainly in relation to rainfall-influenced soil types. The ecoregions of the Great Plains grassland are not the only grassland areas that need redefinition. Equally important for grassland biogeography are those grass stands of limited extent, such as oak savanna, that are embedded in much more extensive forested regions and which support notable grassland-endemic faunas (Hamilton 2005). There are two other grassland types in Canada that are rich in endemic short-horned bugs—one western, the other eastern. There are even a few such sites in northern Canada.

In southern British Columbia, the Okanagan and adjacent valleys have 48 grassland-endemic bugs (Hamilton 1999). This fauna is typical of Palouse prairie (a Great Basin ecosystem) that is quite different from the other valley faunas of British Columbia.

Similarly, isolated eastern grasslands on alvars (limestone plains) in Ontario support 18 grassland bugs not otherwise known from the Great Lakes forests (Hamilton 1997*a*, Bouchard and others 2001). Alvars are tiny compared to the Okanagan Valley, but are thought to have persisted from glacial times (Marie-Victorin 1938). This has been confirmed by wingless leafhoppers that have been isolated on island alvars in Lake Huron for 9,000 years (Hamilton 1994).

Short-horned bugs can survive on other very small fragments of habitat. Ross (1970) reported relict grassland faunas on steep, south-facing slopes in regions dominated by boreal forest, and predicted such faunas should occur as far north as Alaska. This has been confirmed by discovery of endemic leafhoppers on similar sites in central Yukon and some endemics in valleys of adjacent Alaska (Hamilton 1997*b*). That south-facing sites can support a bug fauna even during glacial times was shown by the discovery of insect and plant subfossils on Mt-St-Hilaire near Montréal, Québec dating to 10,000 years ago when the surrounding vegetation was still arctic in character (Mott and others 1981). These remains included oak pollen and the oak-specialist treehopper, *Telamona monticola*.

Leafhoppers are particularly useful in biodiversity studies because so many of their species seem to disperse exceptionally slowly. For example, even when grassland leafhoppers occupy an extensive area they show little dispersal across low barriers, such as mountain passes (Hamilton 2002). Perhaps the most slowly dispersing of all leafhoppers are those of the genus *Errhomus*, which are endemic to the Columbia Basin of Washington and Oregon. Since the females are wingless, they can neither surmount forested passes nor cross canyons deeply incised by glacial meltwater (Oman 1987). That the numerous species survived glacial advances *in situ* was inferred by the exact alignment of a suite of extant species along a

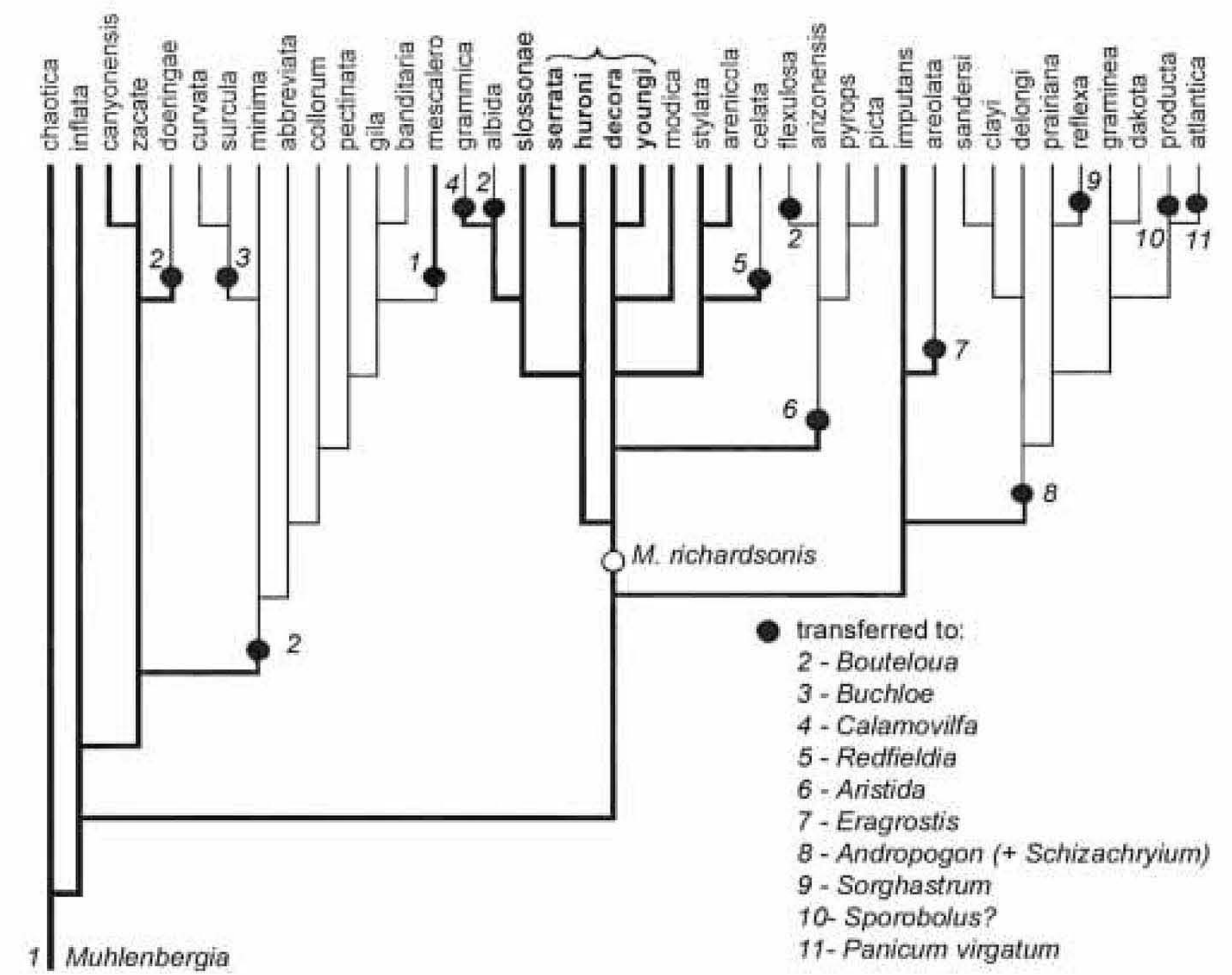

Figure 2. Evolution of *Flexamia*, based on a combination of most distinctive morphological characteristics (Whitcomb and Hicks 1988) and most reliable DNA data (Dietrich and others 1997), with *Flexarida chaotica* as outgroup. Six species (*F. beameri, F. jacala, F. ritanam F. satilla, F. texana, F. zamora*) are not included due to lack of DNA and host information. Ancestral hosts based on oligophagy data, except for those of *F. producta* and *F. atlantica*, which are now polyphagous but could not have evolved on their introduced host grass, *Cynodon*. Ancestral hosts are presumed to be muhly grasses (bold line) until a transfer occurs (black dot). Four *Flexamia* species, bracketed and indicated in boldface, are known only from mat muhly (*Muhlenbergia richarsonis*). Their common ancestor, presumably also on the same host, is indicated by a white dot.

single valley long since erased by geological activity (Hamilton and Zack 1999). Based on this observation and on the present distribution of its closest relatives, *Errhomus praedictus* was discovered within a surveyed area only 60 km across.

Because many leafhoppers specialize preferentially on dominant and subdominant perennial plants characteristic of certain ecosystems, the accumulation of specialist bugs on particular grasses is most probably a measure of long-term dominance within that ecosystem. For example, big bluestem (*Andropogon gerardii*) is usually considered to be dominant on modern tallgrass prairies, although little bluestem (*Schizachyrium scoparium*) has been reported as "the most important native grass in the moist, tall-grass prairie regions" (Odum 1953, p. 306). The latter view is confirmed by leafhoppers in northeastern prairies, six of which specialize on little bluestem, while only one is a specialist on big bluestem (Hamilton 2005).

Long-term associations of leafhoppers and their hosts are evident from phyletic studies. For example, most of the 45 species of the North American leafhopper genus, *Flexamia*, are known to have only one or a very few host plants. Their host genera are identical for many closely related leafhopper species (Whitcomb and Hicks 1988), implying lengthy association with a particular genus of grass. Phylogenetic analysis of 37 species of *Flexamia* (Dietrich and others 1997) has confirmed that the majority of these species have been associated with dominant prairie grasses throughout the evolution of many sequential species (Figure 2).

Deductions

We know very little about the changing paleo-ecological conditions that shaped modern communities and their species throughout the Pleistocene. It is usually assumed that prairies retreated southwards during the height of glacial periods and maintained an equivalent to modern composition and integrity (Ross 1970), while probably extending onto continental margins exposed by falling sea levels during the height of glacial advances (Bennett 1997).

Evidence from northern grasslands does not support this theory, however. While these areas were probably strongly affected by glaciation, they have maintained more than 225 bug species endemic to a greater or lesser area of Canadian plains grasslands (Hamilton 2004*a*). Another 275 endemic bugs in Pacific Northwest intermontane grasslands are even more localized. These probably found at least nine glacial-era refugia close to the ice front (Hamilton 2002). Both grasslands of the plains and of the Pacific Northwest, and the ecosystems around them, were radically affected by glaciation (Matthews 1979, Whitlock 1992) which suggests that none of these refugia could have been untouched by glacial conditions. How, then, did the biota survive?

The effect of Pleistocene climate on insects is best discerned by studying the distribution of flightless leafhoppers, such as *Errhomus calvus* Oman. This species was prevented from moving more than 10 km from the ice front because it lives north of the impassible Columbia Canyon (Hamilton and Zack 1999). It probably survived (as did insects in the Yukon) on steep, south-facing slopes in the canyon where summer insolation raised local temperatures close to those of modern spring time.

Most species of *Errhomus* feed only on balsamroot (*Balsamorhiza sagittata*). This perennial composite is often called "spring sunflower" because it blooms early in the year and withers during the heat of summer. This plant presumably survived on the Columbia Basin during the coldest parts of the Pleistocene by shifting to a midsummer blooming period (Hamilton 2002). It is notable that all but two of the 17 species of *Errhomus* in the Columbia Basin still rely upon this one host.

Another long-standing host association may be seen between muhly grass (*Muhlenbergia* spp.) and all five of the basal lineages of *Flexamia*, plus the out-group *Flexarida chaotica* (Figure 2). This grass was probably the ancestral host for the entire genus.

Furthermore, four species of *Flexamia* (boldfaced in Figure 2) feed only on mat muhly (*Muhlenbergia richardsonis*), a grass common on aspen parkland and intermontane grasslands but not prairies. These four leafhoppers are related, arise from a basal lineage, and probably originally fed on this one grass.

Most of the entire leafhopper fauna of mat muhly is northern. One such leafhopper restricted to mat muhly is *Laevicephalus poudris* (= *L. bison*), which forms a link between many prairie-endemic species and five forest understory species (belonging to the *sylvestris* group, Ross and Hamilton 1972), implying a palaeo-habitat marginal to forest. During glacial advances this grass may have found refugia on sun-warmed south-facing slopes in mountainous areas, and on a semiarid, periglacial grassland close to the ice front on the Great Plains (Hamilton 1994, 2002). Another refugium east of the Great Plains is indicated by the presence of the glacial-age relict, *Flexamia huroni*, in a single prairie fen in Michigan where this leafhopper still feeds on mat muhly (Bess and Hamilton 1999)

The leafhopper genus, *Flexamia*, records in detail a picture of co-evolution of insect and grasslands during at least ten sequential speciation events (perhaps more if extinction was common during the Pleistocene). Such speciation events take a minimum of 50,000 years each in organisms such as diatoms that have brief life spans (Bennett 1997) and at least ten times as long in cicadas (Hill and others 2005) that have brood cycles of nine or more years. Ten or more sequential speciations of annual insects thus ought to represent at least 5 million years, extending the evolution of *Flexamia* well back into the Pliocene or late Miocere when modern prairie ecosystems originated. This time scale has particular significance for the ancestral hosts of *Flexamia*—the muhly grasses.

Although not one species of muhly has been considered as an important component of any modern ecoregion, these plants belong to the most diverse prairie grass genus in the American Southwest, encompassing 45 species as compared to 17 or fewer for any other non-panicoid grass genus (Kearney and Peebles 1964). Its relationship with leafhoppers suggests that *Muhlenbergia* has played a double role: it may have been both diverse and dominant in subtropical Miocene grasslands of North America and, in Pleistocene grasslands, *Muhlenbergia richardsonis* was probably an important and widespread component (it still occurs in scattered localities from the Gulf of St. Lawrence to mountains in Arizona). This particular grass and the bugs that feed on it probably found glacial-age refugia in both the western mountains and far north of more temperate-zone grasslands, creating the disjunct distribution of its specialist leafhopper, *Flexamia serrata* (Whitcomb and Hicks 1988, Figure 30).

Some small, but significant, endemic faunas of previously glaciated areas seem to be composites of insects otherwise found in unglaciated parts of North America. This suggests that northern glacial-age ecosystems were without modern equivalents. In postglacial times these faunas either dispersed to widely separated ecosystems or came together to form unique assemblages. For example, the fauna of grassland leafhoppers on alvars in Ontario is a relict of a 9,000-year-old periglacial ecosystem that has no exact modern equivalent on the Great Plains, being compounded of insects that later dispersed to eastern or northwestern, or even to south-central grasslands (Bouchard and others 2001). Likewise, disjunct grasslands on the Atlantic coast often support prairie-endemic species, although sometimes the seaboard leafhoppers represent a sister-taxon of a prairie species (e.g., in *Neohecalus*;

Hamilton 2000). The fauna of seaboard grasslands is probably an admixture of preglacial and postglacial faunal suites.

Conclusions

Leafhoppers have such intimate associations with dominant and sub-dominant grassland plants, and survive on such tiny grasslands, that they are important indicators of ancient grassland ecosystems. Their inclusion in databases of endemic species will help to define ecoregions on more rigorous criteria, particularly where other data is fragmentary, as in the eastern part of the Canadian prairies.

Searching modern host associations and phyletic histories of bugs reveals very slow ecological changes, suggesting adaptation to certain environmental factors that persisted despite radical environmental changes induced by glacial advances and interglacial warming. Plants with many host-specialist insects, such as leafhoppers, are particularly adapted to survival in the face of potential climate change. Balsamroot, little bluestem, and mat muhly are three such plants with an ancient and important, yet undervalued, role in ecosystems.

Instances of such intensive insect-plant host fidelity can be used to trace the evolution of grasslands since their origins in the Miocene. For example, cooler and drier conditions in the Pliocene are generally credited with fostering widespread temperate-zone grasslands. Ecosystems similar to present-day prairies appear to date this far back. Grasses such as the muhlys, bluestems, three-awns (*Aristida* spp.) and gramas (*Bouteloua* spp.) are the hosts of whole lineages of *Flexamia* (Figure 2), implying ancient patterns of dominance. Most subsequent transfers of *Flexamia* to other genera of grasses seem to be much more recent. Such leafhoppers appear to have transferred mostly to grasses that are adapted to sandy sites (*Calamovilfa* spp., *Redfieldia* spp., *Eragrostis* spp., *Panicum virgatum*) associated with glacial outwashes. These transfers could represent glacial-era changes in leafhopper food-plant induced by local extinctions of dominant grasses in glacier-scoured or coastal areas where prairie grasses that are adapted to rich soils could not survive. Along glacial-front moraines or at continental margins exposed by falling sea levels, sand-inhabiting floras would replace mesic grasses. However, leafhoppers found on prairies as well as along the Atlantic Coast include sister-species that indicate that coastal grasslands had an ancient as well as a modern connection to prairies.

Leafhoppers are clearly an important source of paleo-ecological evidence. While it is too early to state how valuable other short-horned bugs are in such studies, it seems likely that their inclusion can only enhance the data set. It is recommended that ecological databases be expanded to include Homoptera-Auchenorrhyncha before boundaries of ecoregions become fixed as an important component of ecological management decisions.

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