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Unraveling the Enigma of an Atlantic Prairie

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Abstract - The presence of inland grasslands on the Atlantic coastal plain, including an extensive "tall-grass prairie" at Hempstead Plains on Long Island, NY, remote from the "prairie peninsula", has never been explained. In 2008, surveys of Homoptera: Auchenorrhyncha on prairie grasses were conducted from Long Island north to Maine. Multiple prairie-endemic species were found on glades from Rhode Island to New Hampshire, including flightless Cercopidae found only on sand plains. The ranges of 12 species were compared to those of another 50 Cercopidae, Cicadellidae, and Caliscelidae specializing on 15 genera of grasses found in tall-grass prairies. Most support evidence that sand-adapted prairie grasses constitute the easternmost extent of the prairie peninsula that could have come eastward to glaciated New England by following recent glacial moraines before forests re-established themselves in the area 11,000–9000 years ago. This periglacial ecosystem was distinct from a grassland ecosystem in the southeastern states that expanded northwards to Long Island and Cape Cod, MA.

Introduction

The Great Plains of North America are widely acknowledged to support extensive grasslands largely because the Rocky Mountains cast a rain shadow. Eastward, where aridity diminishes, presettlement plains were maintained as grasslands by a combination of fire and the grazing of vast herds of bison. Still farther east, these grasslands become fragmented by forests in river valleys, forming an extensive "prairie peninsula" that extended toward the Great Lakes (Fig. 1A) until being reduced to glades in forests beyond Lake Michigan (Bakowsky and Riley 1994). The Appalachian Mountains (Fig. 1A, purple) separate these grasslands from "barrens" of the Atlantic coastal plains (Fig. 1B, orange), of which the largest northeast of New Jersey (NJ) was more than 13,000 ha just east of New York City at Hempstead on Long Island (Fig. 1C, green). Are these "barrens" remnants of a prairie, or do they represent another kind of grassland altogether?

Other, similar but smaller natural grassy openings, called "heaths", once occurred in many other places in New England, primarily in Massachusetts (MA). These were the breeding grounds for another outlier from the Great Plains, the "Heath Hen", the smaller nominate subspecies of *Tympanuchus cupido* L. (the Prairie Chicken). Heath Hens are now extinct, and their exact historical range is not documented, but they were reported (AvianWeb 2010, NHPTV 2011) from southern Maine (ME) to northern Virginia (VA). Boxborough and Acton are two adjacent places in MA where Heath Hens once lived on extensive grasslands (ACL 2010, TOB 2010). "Heaths" have practically vanished from the east

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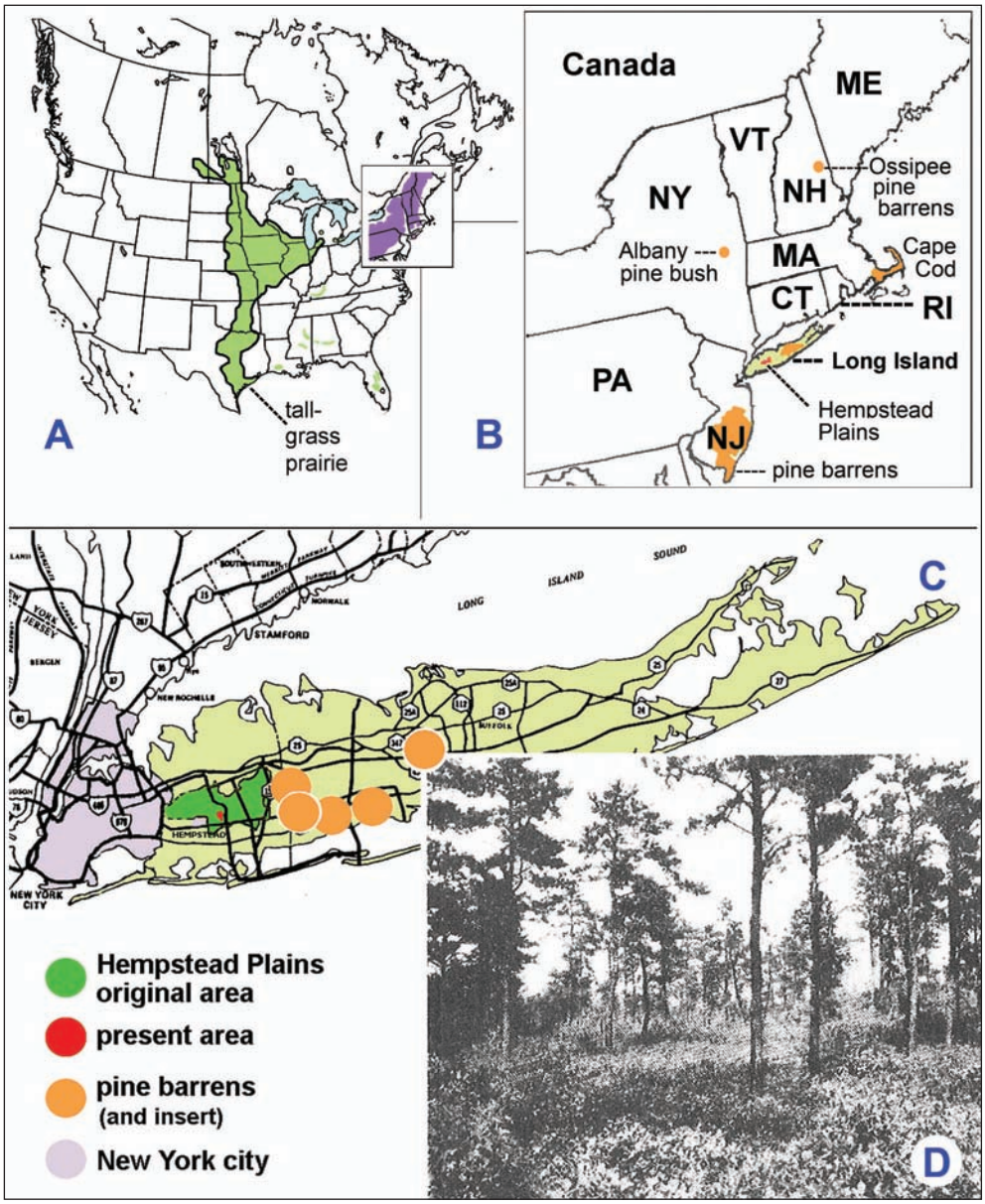
coast, but small glades still remain in widely scattered localities, particularly around pine barrens (Fig. 1D).

So the oddity of Atlantic grasslands broadens to become a complex enigma that includes heaths and glades on the east coast that have undoubted characteristics of prairies. We must consider how prairie plants and wildlife like the Prairie Chicken could have come so far and established a whole ecosystem of grassy plains on the east coast that are not maintained by frequent fires and herds of bison.

Various theories have been advanced since two independent scientists in 1922 discussed the similarities between the floras of the prairies, the Atlantic coastal plain, and the prairie peninsula.



Atlantic coastal plants could have migrated westward up the St. Lawrence River in postglacial times to invade sites with similar climate around the Great Lakes (Peattie 1922).

Prairies could have advanced eastward during a period of heightened aridity followed by fragmentation of the prairie peninsula as postglacial world temperatures waned (Gleason 1922). Westerly dominant winds could account for both the aridity and increased incidence of fire that caused the eastward extension of the "prairie peninsula" (Borchert 1950).

A "periglacial grassland" extending from the prairies to the Great Lakes could have developed south of glacial-age ice margins (Catling and Brownell 1995, Marie-Victorin 1938). Such a situation is not normally considered in palaeoecological reconstructions of ice-age biota based largely on palynology (Matthews 1979), which assume that modern ecosystems merely moved southwards in response to lowered world temperatures.

The northern prairie biota could have found a glacial-age refugium in the south; northward range shifts since postglacial times could have split the flora between lowlands east and west of the Appalachian Mountains (Metzler et al. 2005).

There is also the remote possibility that plants and their dependent fauna have been transported to Atlantic plain sites by human activities.

The purpose of this study is therefore three-fold: (1) to differentiate relict grasslands from those of modern origin, (2) to determine whether prairie grasses came to, or from, the New England states, and (3) to discover how prairie grasses could have crossed or circumvented the Appalachians. Conservation priorities and strategies could be affected by the results of such an analysis.

Since many of the remaining grasslands in New England are mere glades, it is important to utilize an analytical tool appropriate to very small sites. Phytophagous insects that specialize on prairie vegetation are a natural choice. Insects of the order Homoptera, suborder Auchenorrhyncha (short-horned bugs) make excellent indicators of such sites. The bugs of particular interest are Cercopidae or spittlebugs, Cicadellidae or leafhoppers, and Fulgoroidea or planthoppers, which include numerous specialists on all the common grasses and shrubs of the northeastern plains (Hamilton 1994, Ross 1970, Whitcomb et al. 1987). Leafhoppers

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Figure 1 (opposite page). Extent of grasslands in eastern North America: (A) tall-grass prairies and "prairie peninsula" (green) south and west of the Great Lakes (pale blue), with Appalachian Mountains above 200 m elevation (purple) in the study area (box); (B) detail of study area showing location of Hempstead Plains (red) on Long Island (lime green) and extant "pine barrens" (orange) in New England states; (C) detail of Long Island showing New York City (grey), historical area of Hempstead Plains (green) relative to extant remnant (red) and historical records of adjacent pine barrens (orange); (D) photograph of central pine barrens (from Harshberger 1916). CT = Connecticut, MA = Massachusetts, ME = Maine, NH = New Hampshire, NJ = New Jersey, NY = New York, PA = Pennsylvania, RI = Rhode Island, and VT = Vermont. Locations of southeastern grasslands in (A) from Deselm and Murdock (1993); extant pine barrens in (B) from Northeastern Regional Planning Commissions with Pine Barrens Ecosystems, January 1999; historical records in (C) from Cain et al. (1937).

in particular are highly diverse, with more than 800 species considered to be endemic to the Great Plains (Hamilton 1994, Oman 1949, Ross 1970). They do not disperse quickly, and persist as disjunct populations in very small patches of their hosts even hundreds of kilometers from their source populations (Hamilton 1995a). Their presence in any particular northern site indicates that their host was dominant or subdominant at some time since deglaciation (Hamilton 2005, Hamilton and Whitcomb 2010), and has persisted in the vicinity ever since. Their prairie-adapted fauna, rich in species, indicates coevolution in grasslands dating back to the earliest days of the establishment of grasslands in North America (Hamilton 2006).

Field-Site Description

The Hempstead Plains (Fig. 1C) on Long Island, NY is the largest and best studied of the native grasslands of the New England states. Early floral surveys of the Plains showed that thigh-high grass species characteristic of prairies were dominant, suggesting a "mid-grass" plain similar to that of South Dakota, with only small amounts of taller grasses characteristic of disturbed areas such as seashore sites. However, oral and unpublished sources older than 2 centuries suggest that taller grasses such as *Andropogon gerardii* Vitman (Big Bluestem) and *Panicum virgatum* L. (Switch Grass) were once much more abundant, as in a "tall-grass" prairie like that of Illinois (Cain et al. 1937). Today, the grassland has been invaded by weeds including *A. virginicus* L. (Broomsedge), a grass characteristic of disturbed habitats that is now as abundant (Stalter and Seyfert 1989) as the formerly dominant grass, *A.* (or *Schizachyrium*) *scoparius* Michx. (Little Bluestem). Thus, although opinions differ on the original character of the Hempstead Plains, the historical record suggests that the plains are indeed an outlier of prairie and not a recently disturbed habitat. So the enigma remains: how has this grassland, seemingly transplanted from the eastern edge of the Great Plains, been transported for more than 1000 km to an island, and why has it persisted for so long?

The persistence of this grassland has been linked to the fact that the Hempstead Plains have a thin layer of sandy soil overlying an extensive gravel layer gently sloping to the south, the outwash of a terminal moraine left by retreating Wisconsin glaciation (Cain et al. 1937). It is this highly permeable soil that drains away rainwater and renders the land vulnerable to drought. Furthermore, the surface of unbroken sod under the dominant Little Bluestem has "crustose and fruticose lichens and mosses. This crust, together with the strong root-competition, makes it practically impossible for plants not native to the association to establish propagules" (Cain et al. 1937).

The whole of the inland part of Long Island is similarly vulnerable to drought. For example, there are adjacent "pine barrens" (Fig. 1C) that once extended east for >60 km beyond the eastern edge of Hempstead Plains (Harshberger 1916, Kurczewski and Boyle 2000). These two habitats are entirely different in plant assemblage structure. The "barrens" have a dense shrub layer of dwarf oaks (Fig. 1D), while the Plains formerly had such oaks only widely scattered, and these

are now completely absent. Pine barrens are maintained by frequent fires (Kurczewski and Boyle 2000), but there has been no recorded wildfire on Hempstead Plains since records began in 1784 (Cain et al. 1937).

Methods

Grasses not characteristic of eastern woodlands and disturbed sites were sought for sampling, but surrounding vegetation was also sampled in August 2008 at a time of year when the insect fauna is most diverse. The Hempstead Plains remnant at Garden City and numerous other grassland sites of both natural and disturbed areas (roadsides, powerline cuts, etc.) from Connecticut (CT) and Rhode Island (RI) to ME were sampled. Sites were chosen within glaciated New England to supplement what is already known about the northeastern prairie fauna (see Discussion). The insects found in these sites were compared to the known fauna of CT, ME, and New Hampshire (NH) as represented in the Canadian National Collection of Insects (CNCI) in Ottawa, ON, Canada and recorded in faunal catalogues (e.g., DeLong 1923, Lowry 1933, Osborn 1915). Insects from grassland sites farther south are already well represented in the CNCI.

Sweep sampling is the most productive method of collecting phytophagous insects such as leafhoppers. In general, 100 sweeps per targeted plant species is considered minimal, but since such sampling cannot be strictly quantitative (no two collectors ever produce the same yields), expenditure of greater effort is preferable where herbage is dense, or when additional specimens are required for an authoritative identification. In one case, a site near Ossipee, NH was revisited in 2011 to find the missing male of a rare species.

This survey was performed before analyses of other environmental factors (soils, biota) were considered so that an unbiased record would be the result. For example, localities around Boxborough and Acton, MA were not targeted, even though they were once habitats for Heath Hen. These collections were compared with records of the distribution of host-specific Homoptera in the northeastern prairies (Hamilton 1995a) and are supplemented by data gathered since then from the CNCI. Additional records of *Attenuipyga platyrhynchus* (Osborn) (Shovel-headed Leafhopper) were obtained from Guelph University, ON, Canada. Unless otherwise specified, voucher specimens are deposited in the CNCI. The common and scientific names of the tall-grass prairie-inhabiting host plants and of their short-horned bug specialists listed here in tables are given in full elsewhere (Hamilton and Whitcomb 2010). Distributions of prairie plants in the USA are from Barkley (1977) and from eastern Canada are from Dore and McNeill (1980). Palynological data is not cited because grass pollen cannot be identified to genus, the minimum level of analysis in this study.

Results

Field work in 2008 found 9 species of 59 eastern prairie insects (Table 1, boldfaced) in 25 sites on the Atlantic coastal plain (Fig. 2), and two others had been found in previous collecting in adjacent mountains of eastern NY (Hamilton

1994: site #1) within the glaciated part of eastern North America, principally in bluestem-dominated sites. All of these insects feed on grasses. Those that feed on prairie-adapted sedges and shrubs come no farther east than the Appalachians.

Earlier records confirm that 62 species of Cicadellidae (leafhoppers), Cercopidae (spittle bugs), and Caliscelidae (piglet bugs) are specialists on a particular genus or species of grass typical of northeastern prairies (Table 1). An additional 4 unreported sites from Maryland (MD) to Vermont (VT) sampled earlier are also listed here (Table 2).

The fauna on Hempstead Plains represents only 6 grassland species plus an amalgam of forest-inhabiting and invasive species. Two of the grassland species are widespread in the east, feeding on Broomsedge (a southeastern species) as well as on Little Bluestem. They could have been invasive from disturbed areas.

A pine barren on another site (with lichen crust) at the eastern end of Long Island west of Riverhead had no prairie Auchenorrhyncha, nor did another pine barren site near Ossipee (Fig. 1B) in eastern NH. The latter developed on an extensive plain of sand washed down from the glaciated valleys or "notches" around Mount Washington. The preserved section at Ossipee was dominated by pines, now mostly removed, plus a dense understory of *Quercus ilicifolia* Wangenh (Scrub Oak). The Ossipee barrens themselves, being heavily shaded, did not have a lichen crust. A nearby glade, 1 km east of West Ossipee, had bluestems and a lichen crust and supported a number of prairie Auchenorrhyncha, including the rare *Athysanella incongrua* Baker. This specialist on Little Bluestem was formerly known only from the western prairies and a dubious record from the Appalachian

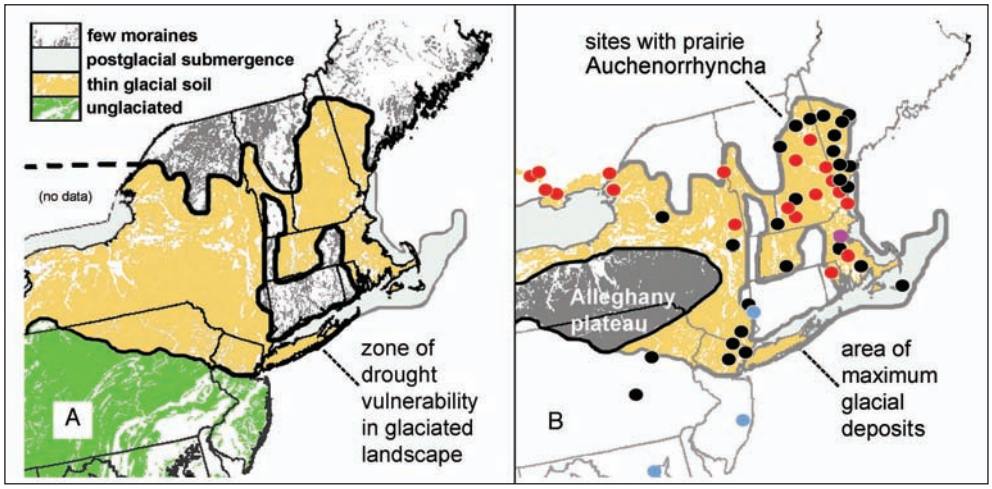


Figure 2. Influence of late Wisconsin glaciation on the Great Lakes and Atlantic seaboard. (A) regional location of glacial moraines (yellow) inferred from zone of soils vulnerable to drought within glaciated territory; (B) eastern sites with prairie Homoptera relative to inferred glacial moraines and outside Alleghany plateau (the earliest glaciated area to be reforested), with alvars of Ontario added, showing by color differential spread from three refugia: blue spots indicate immigration of the spittlebug *Lepyronia angulifera* from the south, a purple spot indicates historical records of the western *Lepyronia gibbosa* in MA, black spots indicate *Prosapia ignipectus* as the only prairie species present, and red spots indicate other prairie species present.

Mountains, a single male reported by Blocker et al. (1988) from Wiley [sic] House in Crawford Notch, NH (Willey House is at 43°49.146'N, 71°10.465'W). This leafhopper is now known from only four short series taken at sites east of Nebraska: (1) the female from the site near Ossipee plus two each of males, females, and nymphs taken there in 2011; (2) three females taken at Hudson Falls, NY by H.H. Ross in 1951 now deposited in the CNCI; and (3–4) two series from North Dakota and Manitoba, taken by the author in 1985 and 1990.

Six other sites (# 1, 3, 8, 10, 27, and 28 in Table 2) are coastal dunes from CT to NH. In addition, four (#2, 16, 19, 26) are bluestem-dominated glades in MA, NH, and RI that have a lichen crust like that of Hempstead Plains. The remaining sites with bluestems in NH are mainly roadside verges, but #17, with 3 prairie endemics, consists of low sand hills along a powerline cut.

Throughout New England, the most frequently encountered prairie-endemic Auchenorrhyncha inhabiting such sites are usually spittlebugs.

Table 1. Northeastern prairie grasses and their specialist Auchenorrhyncha (Cicadellidae, except for *Caliscelidae, †Delphacidae, and **Cercopidae) with species specializing on prairies grasses in New England states (RI–ME) boldfaced.

Host	Auchenorrhyncha specialist
Agropyron and *Elymus* spp.	1. *Athysanella attenuata*, 2. *Attenuipyga minor,* 3. *A. platyrhynchus*, 4. *Commellus comma*, 5. *C. sexvittatus,* and 6. *Mocuellus americanus*
Andropogon/ *Schizachyrium* spp.	**7.**Philaenarcys killa, 8.**Prosapia ignipectus,** 9.*Bruchnomorpha dorsata*, 10.*B. jocosa*, 11.*B. keidensia*, 12. ***Athysanella incongrua***, 13. *Chlorotettix spatulatus*, 14. *Flexamia dakota*, 15. *F. delongi*, 16. *F. graminea*, 17. *F. prairiana*, 18. ***Laevicephalus unicoloratus***, 19. *P. lobatus*, 20. ***Polyamia caperata***, and 21. ***Stirellus bicolor***
Bouteloua spp.	22. *Flexamia abbreviata*, 23. *F. albida*, 24. *F. flexulosa*, 25. *F. pectinata,* 26. *Laevicephalus minimus*, 27. *Paraphlepsius altus*
Calamovilfa longifolia	28. *Athysanella terebrans*, 29. *Flexamia grammica*, and 30. *Laevicephalus exiguus*
Distichlis stricta	31. *Athysanella kadokana*, and 32. *Lonatura salsura*
Hordeum jubatum	33. *Psammotettix knullae*
Koeleria macrantha	34. *Amblysellus acuerus,* 35. *Auridius helvus,* and 36. *Rosenus cruciatus*
Muhlenbergia richardsonis	37. *Flexamia decora*, 38. *F. serrata*, 39. *F. stylata*, 40. *Laevicephalus poudris*, 41. *Lonatura megalopa*, 42. *L. teretis*, 43. *Memnonia anthalopus*, and 44. **Peltonotellus bivittatus*
Panicum virgatum	45. ***Flexamia atlantica,* 46. *Chlorotettix fallax*, 47. *Graminella aureovittata***, 48. *G. mohri*, 49. *G. oquaka*, and 50. *G. pallidula*
Puccinellia nutalliana	51. *Deltocephalus serpentinus*, and 52. *Laevicephalus saskatchewanensis*
Spartina spp.	53. *Destria crocea*, 54. *Neohecalus magnificus*, 55. *Pendarus magnus*, 56. **Aphelonema simplex,* and †57. *Prokelisia crocea*
Stipa spp.	58. *Commellus colon*
Sorghastrum nutans	59.*Bruchomorpha extensa,* and 60. *Flexamia reflexa*
Sporobolus heterolepis	61. *Aflexia rubranura*, and 62. *Memnonia panzeri*.

Table 2. Unpublished records of 12 northeastern prairie Auchenorrhyncha (Cicadellidae, except for *Caliscelidae and **Cercopidae) collected from sites in New England states (NY–ME) and Maryland (MD) by the author (KGA), D. Chandler (DC), V. Thompson (VTh), and R.F. Whitcomb (RFW). Significant records boldfaced.

Site	Collected	Fauna
CT		
(1) 3 km SW Noank 41°19.187'N,71°59.966'W	5 Aug. 2008 KGA	***Chlorotettix fallax, Graminella aureovittata, G. pallidula***
MA		
(2) Lakeville E of I-495 41°54.082'N,70°58.838'W	7 Aug. 2008 KGA	*****Philaenarcys killa**, Polyamia caperata*
(3) 7 km E Ipswich 42°40.996'N,70°46.004'W	7 Aug. 2008 KGA	***Chlorotettix fallax, Graminella pallidula***
MD		
(4) Soldiers Delight NEA	27 Sept. 1989 KGA + RFW	****Bruchomorpha extensa***
ME		
(5) 2 km S Newry 44°27.959'N,70°48.064'W	17 Aug. 2008 KGA	*****Prosapia ignipectus***
(6) Newry jct. Hwy 2+26 44°29.300'N,70°47.045'W	17 Aug. 2008 KGA	*****Prosapia ignipectus***
NH		
(7) South Ackworth	23 Aug. 1979 KGA	*****Prosapia ignipectus***
(8) Seabrook Beach 42°52.9–53'N,70°5.16–5.2'W	13 Aug. 2008 KGA	*****Philaenarcys killa***
(9) Portsmouth tidal flat 43°03.11'N,70°46.20'W	13 Aug. 2008 KGA	***Graminella aureovittata***
(10) 2 km SE Portsmouth 43°02.507'N,70°42.963'W	13 Aug. 2008 KGA	***Chlorotettix fallax, Flexamia atlantica***
(11) Guild E edge of town 43°22.737'N 72°06.994'W	14 Aug. 2008 KGA+DC	*****Prosapia ignipectus***
(12) 6 km N Marlow 43°10.257'N,72°13.108'W	14 Aug. 2008 KGA+DC	*****Prosapia ignipectus**, Polyamia caperata*
(13) 2 km SE Hancock 42°56.914'N,71°57.870'W	14 Aug. 2008 KGA+DC	*****Prosapia ignipectus**, Polyamia caperata*
(14) Pinkham Notch 44°15.397'N,71°15.142'W	15 Aug. 2008 KGA+DC	*****Prosapia ignipectus***
(15) 5 km N Conway 44°01.062'N,71°07.790'W	15 Aug. 2008 KGA+DC	*****Prosapia ignipectus***
(16) 1 km E of W Ossipee 43°49.757'N,71°12.017'W	15 Aug. 2008 KGA+DC	*****Philaenarcys killa**, **Prosapia ignipectus**, **Athysanella incongrua**, Laevicephalus unicoloratus, Polyamia caperata, Stirellus bicolor*
(17) 6 km N Rochester 43°20.985'N,70°59.106'W	15 Aug. 2008 KGA	*****Philaenarcys killa,**Prosapia ignipectus,** Stirellus bicolor*
(18) Plymouth 43°47.245'N,71°47.515'W	16 Aug. 2008 KGA	*****Philaenarcys killa**, **Laevicephalus** unicoloratus*
(19) 1 km W of Quince 43°47.245'N,71°47.515'W	16 Aug. 2008 KGA	*****Philaenarcys killa, **Prosapia ignipectus,** Laevicephalus unicoloratus*
(20) Haverhill 44°06.912'N,72°02.389'W	16 Aug. 2008 KGA	*****Prosapia ignipectus,** Laevicephalus unicoloratus*

Spittlebugs

If we exclude *Clastoptera* Germar (which is usually placed in a separate family, Clastopteridae), there are only 7 species of Cercopidae on tall-grass prairies and each has its own characteristic distribution. Only the most common of the species on the prairies, *Philaenarcys bilineata* (Say), that ranges north into boreal forests (Hamilton 1982), follows an expected postglacial distribution pattern.

The only prairie species of spittlebug that does not reach the Atlantic coast is *Paraphilaenus parallelus* (Stearns), endemic to the Great Lakes region. It lives in sloughs on the prairies and ranges east from Wisconsin (WI) into alkaline fens in ON (Fig. 3).

The most easily recognized prairie spittlebug is *Prosapia ignipectus* (Fitch), variously and appropriately called the Black Spittlebug or Fire-bellied Spittlebug for its black dorsum and contrasting red-and-black venter (Fig. 4). It ranges from Pennsylvania (PA) and RI north to western ME wherever Little Bluestem occurs, including roadside verges from sea level up to Pinkham Notch at 700 m ASL. It is not found on Big Bluestem, even when that species is dominant and mingled with clumps of Little Bluestem. Although the Black Spittlebug was by far the most commonly encountered prairie species in this study, it was not found at Hempstead Plains. It has been found previously on the western side of

Table 2, continued.

Site	Collected	Fauna
(21) Gorham 44°23.110'N,71°09.722'W	KGA	17 Aug. 2008 *****Prosapia ignipectus***, *Laevicephalus unicoloratus*
(22) 3 km E Jefferson 44°26.177'N,71°30.876'W	17 Aug. 2008 KGA	*****Prosapia ignipectus***
NY		
(23) Woodgate + 7 km W + 5 km SW Otter Lake	19 Aug.1990 KGA	*****Prosapia ignipectus***, *Polyamia caperata*
(24) Garden City (Hempstead Plains) 40°43.4–43.7'N, 73°35.0–35.15'W	4 Aug. 2008 KGA	****Bruchomorpha jocosa, Chlorotettix fallax, Flexamia atlantica, Graminella aureovittata,*** *Laevicephalus unicoloratus, Stirellus bicolor*
(25) Albany Pine Bush	24 Aug. 2008 VTh	*****Philaenarcys killa***
RI		
(26) 4 km NE Clayville 41°47.540'N,71°37.950'W	5 Aug. 2008 KGA	*****Philaenarcys killa, **Prosapia ignipectus,*** *Polyamia caperata, Stirellus bicolor*
(27) 1 km W Jerusalem 41°22.935'N,71°31.542'W	5 Aug. 2008 KGA	***Chlorotettix fallax, Graminella pallidula***
(28) 1 km W Weekapaug 41°19.753'N,71°46.455'W	5 Aug. 2008 KGA	***Graminella pallidula***
VT		
(29) 4 mi W Wilmington	23 Aug. 1979 KGA	*****Prosapia ignipectus***

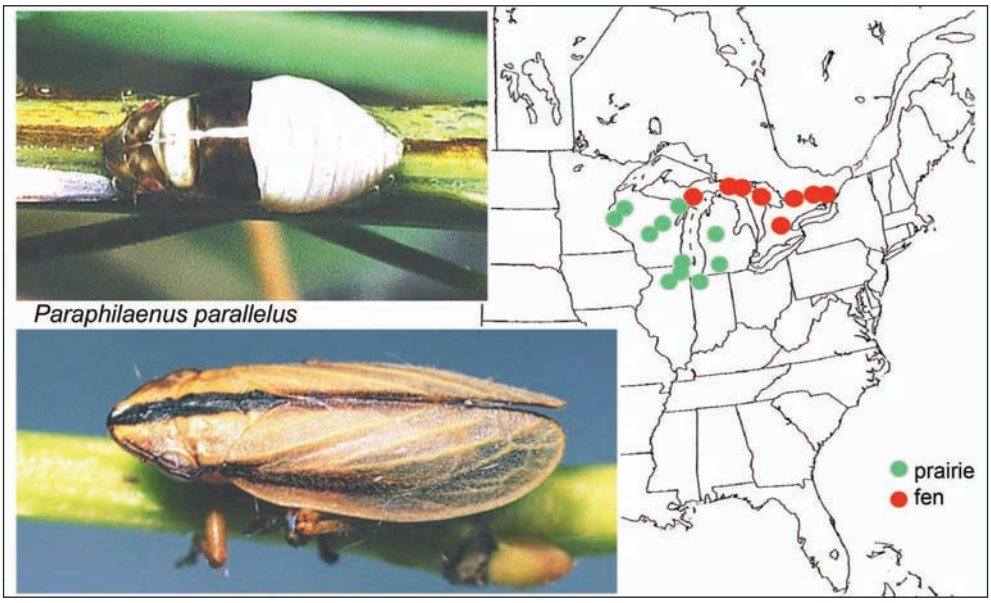


Figure 3. The Fen Spittlebug, *Paraphilaenus parallelus*, nymph and adult (photographs courtesy of S.A. Marshall) and its distributions on prairies (green) and on heaths or alvars in eastern woodlands (red).

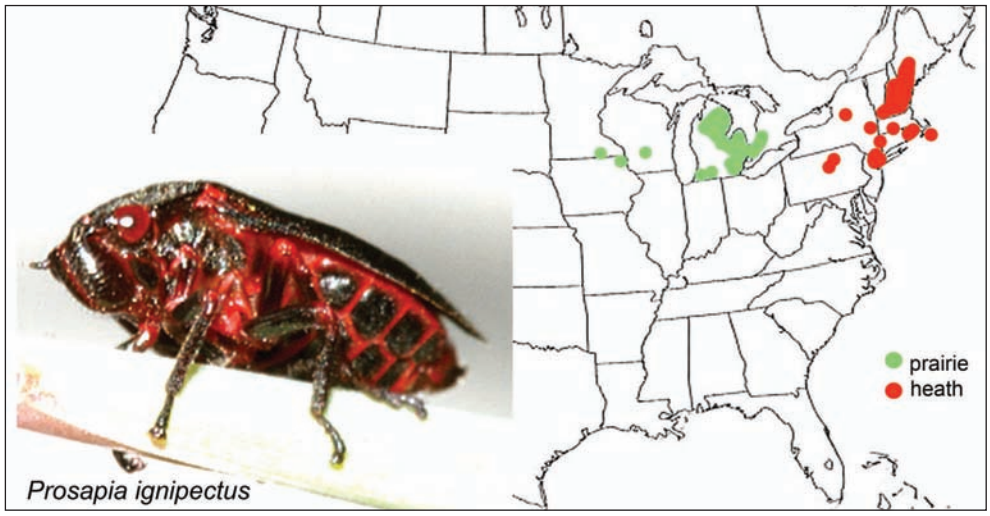


Figure 4. The Black Spittlebug, *Prosapia ignipectus*, showing its striking red leg bases and intersegmental membranes (photograph courtesy of Tom Murray), and distributions on prairies (green) and on heaths or alvars in eastern woodlands (red).

Figure 6 (opposite page, lower). Distribution of *Philaenarcys* species on the Atlantic seaboard and inland sites. (A) the Salt Marsh Spittlebug, *P. spartina*, and its coastal sites (in red); pale green areas indicate the coastal range of its host, and darker green its main host distribution (where this spittlebug does not occur). (B) the Sand Plain Spittlebug, *P. killa*, and its disjunct distributions (only sites where winged specimens were found are in darker green).

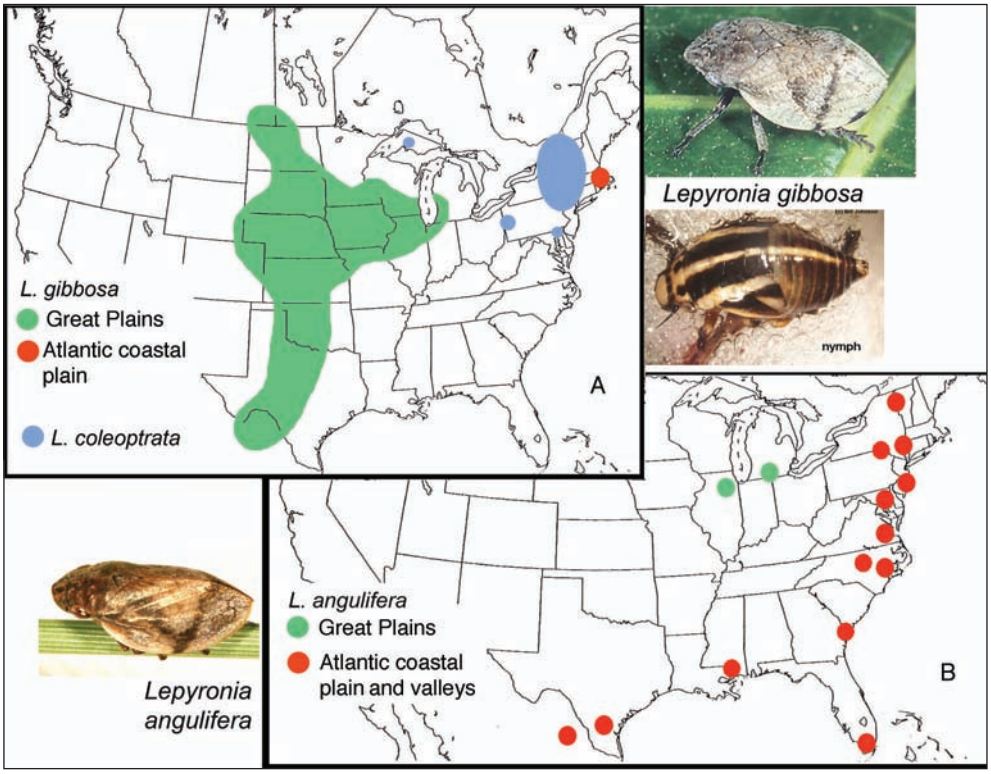
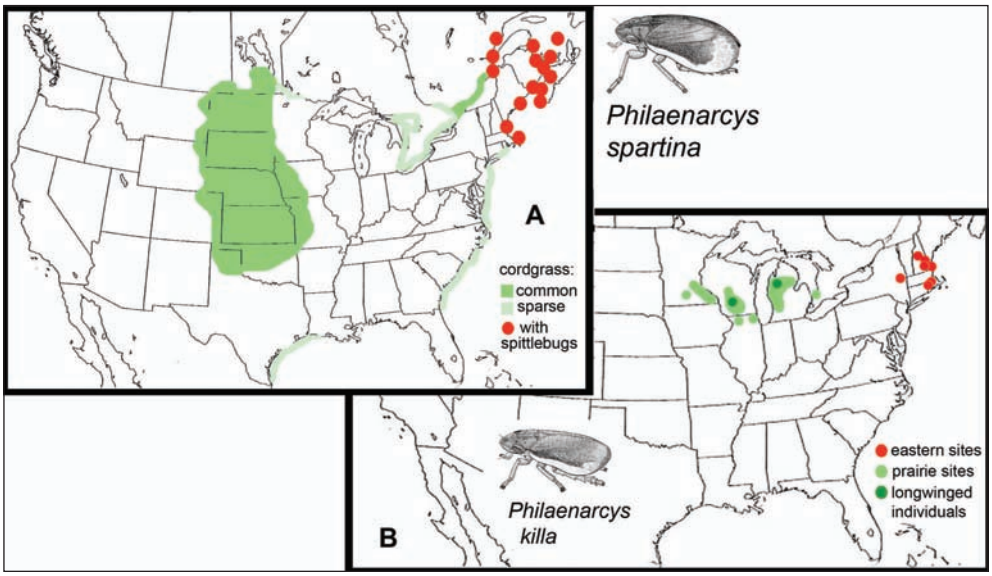


Figure 5. Disjunct spittlebug distributions on Great Plains (green) and on Atlantic coastal plain and associated valleys (red). (A) *Lepyronia gibbosa* (photographs of adult and nymph courtesy of Bill Johnson) and distribution (green) compared to that of *L. coleptrata* (blue). (B) *Lepyronia angulifera* (photograph courtesy of Jim Kramer) and known sites, with Burlington, VT and Hurd Corners, NY verified from photographs contributed by Eiseman (2007) and Kelly (2007); additional sites in Georgia, New York, North Carolina, and Mississippi also from BugGuide.net.



the Adirondack Mountains of upstate NY and in the Hudson Valley down to the river's mouth, but only on the mainland (Hamilton 1982).

Lepyronia gibbosa Ball (Hill Prairie Spittlebug), at 7–10 mm, is equally as large as *Prosapia ignipectus.* It is readily recognized by its ashy grey color and pointed head. Its nymph has prominent black stripes (Fig. 5) which resemble those of the nymph of the introduced *L. coleoptrata* (L.) that occurs over a limited area in NY and VT (Fig. 5A, blue), where the native species does not occur. *Lepyronia gibbosa* was collected over a hundred years ago in a number of sites near Boston, MA (Hamilton 1994). This disjunct population has not been verified and may have been extirpated by intensive human land use.

A smaller species, *Lepyronia angulifera* Uhler (Fig. 5), common in the Caribbean, occurs as far up the Atlantic coastal plain as Burlington, VT in the Hudson Valley and inland to southern Michigan (MI). It has been recorded as far west as Spring Lake, IL (Fig. 5B) according to a photograph by R. Curtis of Chicago, IL taken on 24 September 2008.

The only spittlebug endemic to northeastern North America is *Philaenarcys spartina* Hamilton (the Salt Marsh Spittlebug), which inhabits coastal salt marshes, where it feeds exclusively on *Spartina* spp. (cord grasses), including *Spartina patens* (Ait.) Muhl. (Salt Hay). Its only close relative is *P. bilineata*. These appear to represent a glacial-age disjunction, with the widespread parental species now feeding on various grasses, but not inhabiting cord grasses on the prairies (Fig. 6A).

Philaenarcys killa Hamilton (Sand Plains Spittlebug) is common on the "prairie peninsula" from the southern tip of ON (Fig. 6B; Hamilton 1995a). From Minnesota (MN) eastward, it has been taken only in the presence of Little Bluestem. It was found in seven Atlantic sites in 2008. One specimen was taken in upstate RI, and 61 others from coastal and inland sand plains of MA and NH. The presence of this spittlebug on the Atlantic coastal plain was quite unexpected because the closest prairie populations were 600 km away on the west side of the Appalachian mountains, and because this species is almost always flightless: the hind wings are usually reduced to small, useless flaps under the elytra-like front wings. The only exceptions are 2 populations with winged females near the Great Lakes, one in MI and the other in WI. It is doubtful if even these winged individuals actually fly. Although they constituted about half of their populations (as in other species of *Philaenarcys*), no such winged individuals were found on any nearby site, indicating a lack of gene flow between populations.

Together, these examples represent 5 grasslands-restricted species with 5 different distribution patterns. It is odd that this one small family has the greatest proportion of disjunct prairie species of Auchenorrhyncha in eastern North America, even though one of the species is flightless. This finding probably reflects the greater persistence of spittlebugs in isolated habitats, protected as they are from both desiccation and predators by their nymphal spittle masses.

Planthoppers

The Atlantic plain Fulgoroidea include a number of prairie planthoppers, mainly Delphacidae (Fig. 7A) and Caliscelidae (Fig. 7B). The planthoppers

that inhabit grasslands are best known from the rich fauna associated with cord grasses (Beamer 1950, McDermott 1952, Wilson 1982). The rest are usually of two kinds: either common and widespread, or rare and widely scattered. *Muirodelphax parvulus* (Ball) (= *Delphacodes rotundata* Crawford) represents the first, being one of the most abundant of Delphacidae in Missouri tall-grass prairie (Wilson et al. 1993) and found everywhere bluestems occur. They are highly vagile and able to locate isolated patches in the boreal forest of northern MI and MN and even High Park in Toronto, ON (K.G.A. Hamilton, unpubl. data). The second kind includes *Bruchomorpha extensa* Ball that is known only from few sites in Arizona, California, North Carolina, New Mexico, Texas, and Utah (Brimley 1938, Doering 1940) and is rare on the prairies, probably restricted to remnants of glacial-age grasslands. It has recently been found in MO and WI and also in MD on Indian Grass.

Why so many planthoppers are scarce in collections is probably an artifact of collecting. We probably need a vacuum collector to effectively sample insects such as these that favor root crowns as safe breeding sites. Caliscelidae, though fewer in number of species, are more abundant in collections because they are readily taken with a sweep net.

Nine of 11 northern Caliscelidae inhabit only the prairie provinces of Canada (Maw et al. 2000) and adjacent areas in the United States, and 3 of these exhibit ranges indicating their spread across the Mississippi River to the southeastern states and subsequent dispersals northwards. *Bruchomorpha jocosa* Stål is the most widespread of these and is even more abundant than *M. parvulus* (Wilson et al. 1993). *Bruchomorpha jocosa* has a southeastern subspecies *obscura* Ball that was found at Hempstead Plains. This is the northernmost record for this insect and is also a new state record.

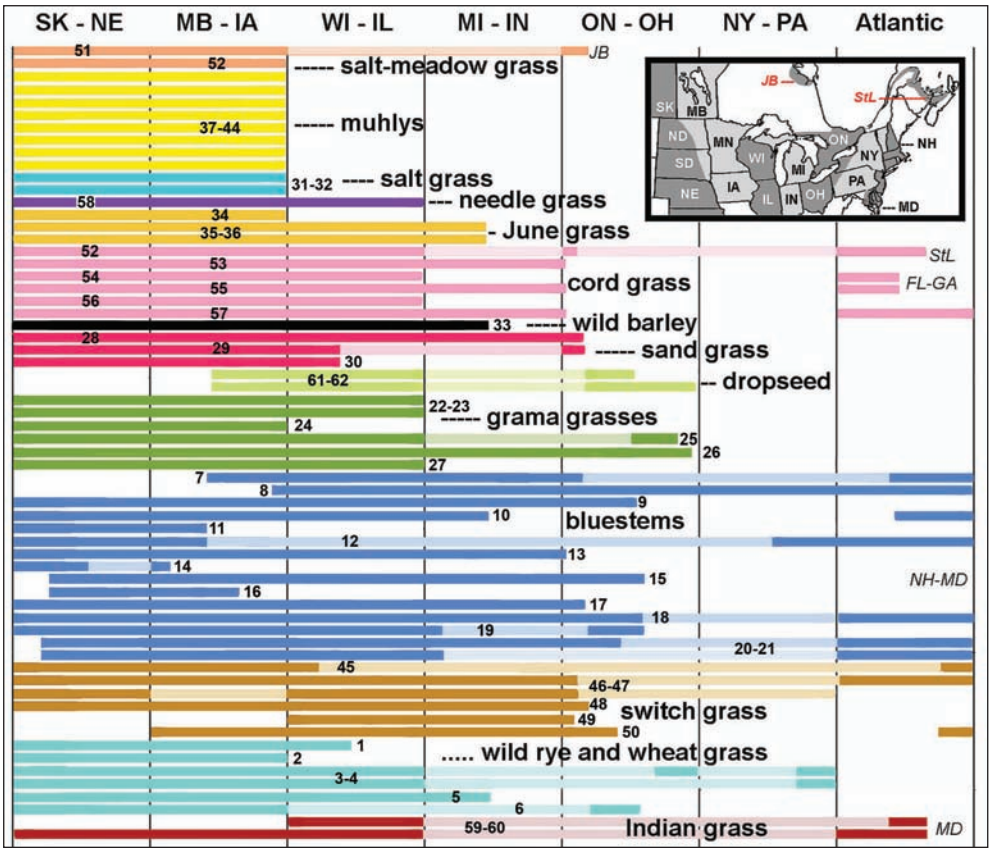
Leafhoppers

Other prairie species of Auchenorrhyncha are mainly leafhoppers (Table 1). Those that are also found on the Atlantic coastal plain display the same range of distribution patterns as Cercopidae (Figs. 3–6). Most frequently, they are limited to sites north of Long Island, with scattered records from montane valleys between the Atlantic coastal plain and the "prairie peninsula". Only a few species are found on isolated coastal sites no further south than northern VA, or are southeastern grassland insects ranging north along the coast. A single prairie species has been found also on the shores of James Bay (Fig. 8).

All but 1 of the new state records from Hempstead Plains are leafhoppers of the genus *Flexamia* (Whitcomb and Hicks 1988): *F. areolata* (Ball) on *Eragrostis* (love grasses) previously reported from CT and NJ; *F. atlantica* (DeLong) on the Hempstead Plains confined to Switch Grass in open oak woods, as it is at Cape Cod, MA; and *F. sandersi* Osborn on Broomsedge, previously from MA and MD. *Flexamia atlantica* has the same distribution as the subspecies of Prairie Chicken and Heath Hen, with broad distribution on the Great Plains and an isolated population in the east that is characteristic of coastal grasslands from southern NJ north to Cape Cod (Whitcomb and Hicks 1988).

Leafhoppers may be conveniently grouped by their grass hosts (Fig. 8) because so many of the northern fauna are monophages (Hamilton and Whitcomb 2010). For example, those that feed on *Agropyron* (wheatgrasses) and sometimes also on *Elymus* (wild ryes) are frequently found together. The farthest eastern site for

Figure 7. (A) *Muirodelphax parvulus* (Ball), the most abundant planthopper on Little Bluestem and Broomsedge (photograph © Ron Meldar); (B) *Bruchomorpha extensa* Ball, an eastern disjunct in MD on Indian Grass (photograph © Tyler C. Christensen).



wheatgrass-feeding leafhoppers, a glade east of Elizabethtown, NY (Table 2) was found to have 2 distinctive species: *Commellus comma* and the Shovel-headed Leafhopper (Figs. 9, 10). These are more than 200 km from the nearest sites to the west (Hamilton 1995b, 2000).

Andropogon and *Schizachyrium* (bluestems) are the favored grass hosts for most tall-grass leafhoppers, and a large proportion of these range into the east (Fig. 8). Little Bluestem is the favored host, but some of these specialists will also survive on Broomsedge, which has its own specialists as well. Only one leafhopper is known from Big Bluestem on the northern plains: *Flexamia prairiana* DeLong. In the southern states, this leafhopper will also accept Little Bluestem. Southern populations of leafhoppers often have broader host ranges than in northern sites (Hamilton and Whitcomb 2010).

Bouteloua (grama grasses) are almost entirely western, and the only leafhoppers associated with them in the east are both on *B. curtipendula* (Michx.)Torr. (Sideoats). *Flexamia pectinata* (Osborn & Ball) ranges as far east as Ohio (OH). *Laevicephalus minimus* (Osborn and Ball) is a more exceptional disperser. Its

Figure 9. *Commellus comma* (Van Duzee) (photograph courtesy of Chris Dietrich).

Figure 10. *Attenuipyga platyrhynchus* (Osborn), which shares the same easternmost site in NY as *Commellus comma* (photograph courtesy of Christopher Dietrich).

Figure 8 (oppostie page, lower). West-to-east distribution of 60 species of eastern Auchenorrhyncha specializing on prairie grasses, from 7 longitudinal zones (map inset). Full color bars indicate confirmed records; pale color indicates probable occurrence. Grass hosts (color) ranged from westernmost genera (saltmeadow grass, *Puccinellia*; muhly, *Muhlenbergia*; salt grass, *Distichlis*) to prairie peninsula grasses (needle grass, *Stipa*; June grass, *Koeleria*; cord grass, *Spartina*; wild barley, *Hordeum*; sand grass, *Calamovilfa*; dropseed, *Sporobolus*; grama grasses, *Bouteloua*; rye and wheatgrasses, *Elymus / Agropyron*), and widespread grasses (bluestems, *Andropogon / Schizachyrium*; switch grass, *Panicum virgatum*; Indian grass, *Sorghastrum*).

diminutive adults are able to successfully track individual plants in patches separated by more than 200 km in southern ON (Hamilton 1995a). Neither this grass nor its leafhopper has been found in the study area.

Spartina (cord grasses) are mostly populated with various planthoppers along the Atlantic coast, with three delphacid species: *Megamelus metzaria* Crawford and *Prokelisia dolus* Wilson ranging from the Atlantic inland as far as ON (Maw et al. 2000), and *P. crocea* (Van Duzee) found as far west as Colorado (Wilson 1982). These grasses also have a well-associated leafhopper fauna in the prairie peninsula and the Gulf of St. Lawrence south along the Atlantic coast as least as far as Cape Cod. A single record of *Destria crocea* (Beirne) from the Great Lakes (near Escanaba, MI) suggests that the eastern and western populations may once have been connected through the St. Lawrence valley. However, a recent dispersal is questionable, since another cord grass specialist *Neohecalus lineatus* (Uhler) is confined to the coast, while its sister species *N. magnificus* Hamilton is found only on the prairies (Hamilton 2000), suggesting a vicariant event in the distant past.

Sporobolus (dropseeds) have several specialist leafhoppers in the east, but only *S. heterolepis* Gray (Northern Dropseed) has a prairie fauna of two leafhoppers that extend their range into eastern woodlands. These flightless insects are usually found together on alvars (limestone plains around the Great Lakes that support prairie vegetation), but have not been found where their host inhabits alkaline fens in southern MI.

Other grasses adapted to saline flats, such as *Distichlis stricta* (Torr.) Rydb. (Alkali or Salt Grass) and *Puccinellia nuttalliana* (Schultes) Hitchc. (Salt-meadow Grass) only occur east of the tall-grass prairie on coastal sites. Most species of *Muhlenbergia* (muhlys) and their many leafhoppers are confined to the prairies, with the exception of a few alkaline fens in southern MI, where a disjunct population of *M. richardsonis* (Trin.) Rydb. (Mat Muhly) supports an endemic leafhopper, *Flexamia huroni* (Bess and Hamilton 1999).

There are three leafhoppers on *Koeleria macrantha* (Ledeb.) Schultes (June Grass) and all of them are widespread on sandy or arid areas of the prairies and prairie peninsula, but like their host do not spread farther east. *Stipa spartea* Trin (Needle Grass) and *Hordeum jubatum* L. (Wild Barley), similarly growing on droughty soils, each have a single specialist leafhopper that occurs throughout the prairie peninsula, but does not seem to follow a host which spreads readily down highway corridors to eastern sites.

By contrast, sand-loving grasses often show disjunct distributions. *Calamovilfa longifolia* (Hook) Scribn. (Sand Reed Grass) has two disjunct stands, one on the east side of Lake Michigan and the other on the south side of Lake Huron up the east side as far as the Bruce Peninsula. One prairie species, *Athysanella terebrans* Gillette and Baker, is found on both stands. *Laevicephalus exiguus* Knull on the Bruce Peninsula, ON is a leafhopper that has transferred from the western dominant grass *Buchloë dactyloides* (Nutt.) Engelmann (Buffalo Grass) to Sand Reed Grass (Hamilton and Whitcomb 2010), probably during the last glaciation.

Similarly, Switch Grass is widely disjunct between the prairies and the coast. It supports mostly leafhoppers of the genus *Graminella* (Table 1; Hamilton and Whitcomb 2010), of which two occur in the study area: *G. pallidula* (Osborn), a Great Lakes species found at four sites in CT, MA, and RI, and the widespread *G. aureovittata* (Sanders and DeLong). The latter was found at two coastal sites in CT and NH, plus Hempstead Plains; it is known also from MA as well as the Gulf states and IL (Kramer 1967). I have found it also on the last remaining grassland on the Marblehead alvar in OH at the western end of Lake Erie. Another leafhopper specialist on Switch Grass, *Chlorotettix fallax* (Sanders and DeLong), was found in four coastal locations of CT, MA, NH, and RI—the first time it has been recorded north of VA and east of IL. It is mainly a prairie species, found from the Gulf coast north to Nebraska (specimens collected by R.F. Whitcomb, in CNCI) and also at Windsor, ON.

Sorghastrum nutans L. (Nash) (Indian Grass) occurs sparsely across eastern grasslands and ranges into the southern states. Its only specialist leafhopper, *Flexamia reflexa* (Osborn and Ball), like its host, is rather sparsely found throughout eastern grasslands (Whitcomb and Hicks 1988), but was not found in the study area.

Discussion

There has been no documented case of Auchenorrhyncha that specialize on prairie grasses being transported by human activities to new sites, even during prairie reconstruction projects. Only a few prairie Homoptera—the spittlebug *Prosapia ignipectus*, the leafhoppers *Laevicephalus unicoloratus* (Gillette & Baker), *Polyamia caperata* (Ball), and *Stirellus bicolor* (Van Duzee), and the planthopper *Muirodelphax parvulus*—were found in disturbed sites in the study area. These were mainly from roadside verges where bluestems were common. They are clearly differentiated from the many species that are restricted to grassland remnants. The use of such grass-specialist insects to identify relict grasslands thus satisfies the first objective of this study, to differentiate older, remnant grasslands from those of modern origin.

Analysis of the ranges of Auchenorrhyncha specializing on prairie grasses shows an overall reduction of the fauna eastward. Of 62 species found on northeastern prairies, 40 inhabit the “prairie peninsula” of IL and WI, 25 are found in MI and northern Indiana (IN), and a similar number (but different in composition) in ON and OH (Hamilton 1995a). Only four are known from NY and PA. The second objective is therefore satisfied: the most abundant prairie grasses came to the New England states from the prairies rather than by traveling inland from the coast, and the theory of Peattie (1922) of east-to-west dispersal along the Saint Lawrence River is not clearly supported by overall insect data. However, it must be acknowledged that the evidence is conflicting for the flora and fauna of several grasses. Indian Grass has a disjunct fauna of Auchenorrhyncha without northeastern relicts. Also, *Spartina* (cord grasses) could have come both from

the Atlantic coast up the St. Lawrence River, as suggested by the ranges of the planthoppers *Megamelus metzaria* and *Prokelisia dolus*, and northwards along the Atlantic coastal plain from the southeastern states, as suggested by the range of *P. crocea*. Furthermore, invasion of the east coast cord grass beds from inland sites may have occurred at some earlier interglacial period, because the northern Atlantic coast *Spartina* beds support *Neohecalus lineatus*, a "sibling" species (close relative) of the prairie-inhabiting *N. magnificus*. There are several less well-documented examples of other Atlantic disjuncts of Auchenorrhyncha in the Maritime provinces of Canada. However, grasses such as *Sorghastrum* and *Spartina* form a small subset of the prairie flora, and their few associated insects are usually limited to the coast of, respectively, Cape Cod and Long Island southwards (Fig. 5) or from the Gulf of St. Lawrence to the Bay of Fundy inland to the Great Lakes (Fig. 6A).

Theories of floral dispersals

Gleason (1922) first postulated an eastward postglacial expansion of the prairies during a period of heightened aridity (the Xerothermic hypothesis). This hypothesis has been supported by numerous studies of pollen cores from lake bottoms and bogs which show an expansion of grass and *Artemisia* pollen, suggesting that postglacial temperatures may have been higher than now. Such an "Altithermal" or "Hypsithermal" expansion of the Great Plains could explain why there are at least 55 areas in southern ON that support prairie vegetation representing less than 4% of an estimated 530 km^2 that existed before European settlement (Bakowsky and Riley 1995). The possibility that the prairies could have extended across OH and PA to the coast has been discussed (Mehrhoft 1997). However, the Xerothermic hypothesis is not supported by any of the distribution patterns of Auchenorrhyncha. The "true prairie" is differentiated clearly from the prairie peninsula by the presence of more than 10 prairie insect species on arid-adapted plants such as *Artemisia* (Hamilton and Whitcomb 2010), Mat Muhly, Salt-Meadow Grass, and Salt Grass, none of which has been found to have associated Auchenorrhyncha east of the Mississippi River (Fig. 8). While such plants (and their insect fauna) may be found northwards in sandy areas of boreal forest, possibly as a result of postglacial temperatures being higher formerly than they are today, there is scant evidence that higher temperatures necessarily resulted in greater drought sufficient to expand prairies much farther eastward. For example, the extent of pine forests during the Altithermal (ca. 7000 BP) was similar to that of today, and intensification of herb dominance at that time occurred only as far east as western Iowa (Bernabo and Webb 1977). Conversely, the Altithermal was accompanied by an increase in *Pinus strobus* L. (White Pine) at the expense of grassland in southern Ontario; in fact, such sites did not become fire-maintained oak savannah until after the Altithermal (Szeicz and MacDonald 1991).

There is some support for a west-to-east biological connection between the Great Lakes and the Atlantic coastal plain by way of the St. Lawrence River.

For example, a dune-inhabiting moth, *Euxoa detersa* (Walker), ranges from the Nebraska sandhills east to sandy areas along the St. Lawrence River, while a separate subspecies confined to the Atlantic coast suggests an earlier interglacial dispersal eastward along this corridor (Lafontaine 1982). However, no Auchenorrhyncha show such a distribution pattern for sand-associated plants, only for semiaquatic species. For example, cord grasses show a connection between the Great Lakes and the Atlantic coast by way of the St. Lawrence River (Dore and McNeill 1980). Four species of Auchenorrhyncha specializing on cord grass have traveled east as far as IL (Fig. 8), of which 2 are found near the Great Lakes at Windsor, ON and also on the shores of the Gulf of St. Lawrence. It is likely, therefore, that before the glacial-age carving of the Great Lakes, these insects found enough cord grass along that former drainage basin to migrate from WI to the Gulf of St. Lawrence but, requiring saline flats, cord grass now has a scattered distribution on the Great Lakes (Dore and McNeill 1980) inimical to leafhopper

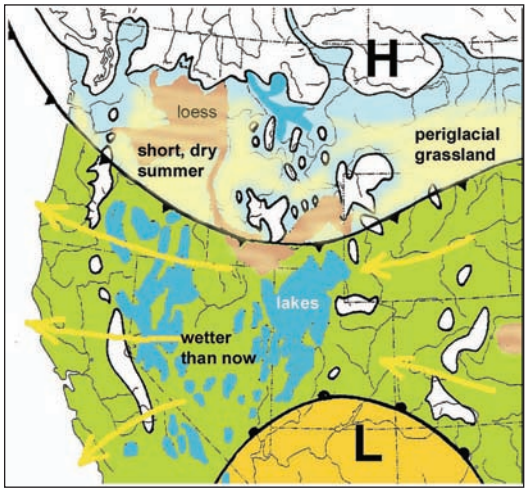


Figure 11. Postulated Pleistocene environment with glacial age summer monsoon over western USA (redrawn from Hamilton 2002), with permanent high pressure (H) system over Canada and low pressure (L) over southwestern states, together driving east-to-west air flow creating heightened rainfall and glacial lakes across intervening areas (except for ice-dammed Glacial Lake Missoula in Montana), contrasting to arid conditions over Pacific Northwest.

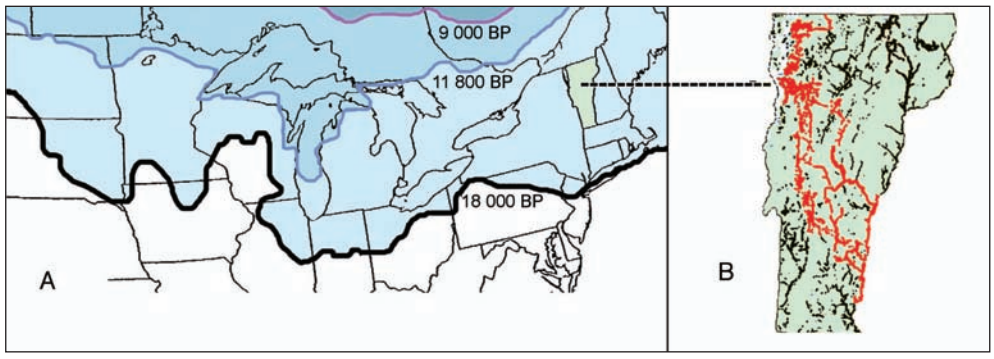


Figure 12. Glacial influences in the study area. A) Maximum glaciation at 18,000 BP (blue area) showing glacial ice margin during last advance at 11,800 BP (blue line) and when the Great Lakes regained their current lake level at 9000 BP (purple line). B) Detail of VT showing the most probable postglacial connections between eastern and western sand plains.

dispersal. More vagile insects such as moths can fly long distances across areas of patchy vegetation.

Northward range shifts of prairie species in postglacial times splitting their ranges between lowlands east and west of the Appalachian Mountains (Metzler et al. 2005) would require a glacial-era refugium in Alabama/Florida or perhaps in Texas/Oklahoma, and indeed, grasslands existed on both sides of a boreal forest along the Mississippi Alluvial Valley until at least 15,000 BP (Brown 2003). Either scenario requires any northern fauna to be very vagile to cross the Mississippi River at a time when it would be carrying vast quantities of glacial meltwater and when there were lowered summer temperatures across the whole region (Kurczewski 2008). Thus, a glacial-age crossing would be impractical for most grasses adapted to northern prairies, and many of their specialist insects as well. Such isolated glacial-age grasslands were probably very different in biotic composition. It is likely that prairies expanded to the eastern side of the Mississippi Valley during an interglacial period (perhaps the Sangamon, 120,000–150,000 BP) when world temperatures were higher than at any time after the most recent (Wisconsin) glaciation, and only widespread or southern fauna could make the transfer. Evidence from insect surveys of "black soil prairies" in Alabama and Mississippi suggest that relatively few Auchenorrhyncha made this transition, and those that did are often subspecifically different, as is the Heath Hen.

By contrast to these other theories, the periglacial "sidewalk" theory (Marie-Victorin 1938) is both validated by this study, and is particularly crucial to explaining the considerable number of northern Auchenorrhyncha characteristic of prairies that migrated into the prairie peninsula and from there to the Atlantic seaboard.

The presence of hundreds of endemic Auchenorrhyncha on northern prairies and intermontane valleys (Hamilton 2002) confirm that a periglacial grassland, probably formed by summer monsoon (Fig. 11), was well developed in western North America. This fauna includes flightless species in the leafhopper genera *Aflexia*, *Errhomus,* and *Memnonia*, indicative of a fauna specialized to windy ecological "islands". The study of such flightless insects in alvars on islands of known age indicates that such a northern grassland was present in ON 9000 years ago (Hamilton 1994) when the glacier margins were within a few hundred kilometers farther north (Fig. 12A). Plants characteristic of alvars include Little Bluestem, Northern Dropseed, wheat grasses, *Eleocharis* (spikerushes), and shrubs such as *Juniperus horizontalis* Moench (Creeping Juniper) and *Prunus pumila* L. (Sand Cherry), all of which support leafhoppers characteristic of northern prairies (Hamilton and Whitcomb 2010).

Also common on the northern prairies is *Salix exigua* Nutt. (Sandbar Willow), which is also found in valleys as far east as NH along with its associated leafhoppers (Hamilton 1980, 1983), so it may also have been part of this flora. By contrast, Sideoats, Sand Reed Grass, and Wild Rye are more southerly plants that probably invaded moraine grasslands at a later date when the Appalachian Mountains were already forested.

Evidence of faunal dispersals

Turning to the third objective, to discover how prairie grasses could have crossed or circumvented the Appalachians, we need to examine how their associated insects are distributed. In that context, it is noteworthy that both the common grassland spittlebugs in the New England states, *Prosapia ignipectus* and *Philaenarcys killa*, mirror the same distribution pattern. Their ranges (Figs. 4, 6B) seem to indicate that they had migrated eastward through VT to NH.

Like *Prosapia ignipectus*, *Philaenarcys killa* was verified in this study as host-specific on bluestems and restricted to northern grasslands in eastern North America. It occurs in all four bluestem-dominated glades in MA, NH, and RI that have a lichen crust like that of Hempstead Plains; but it was not found in Long Island at all. Additional specimens from Concord and Durham, NH were found in the University of New Hampshire collection misidentified as the northern *P. bilineata* (Say), along with a similarly misidentified specimen of *P. spartina* from the coast. Additional specimens from NY in the vicinity of the Albany pine bush were taken by V. Thompson, also in 2008, suggesting that this flightless species traversed the mountains of VT in postglacial times by way of interconnecting valleys (Fig. 2).

Since *Philaenarcys killa* does not disperse rapidly and is always found only on sand plains and dunes, it must have come to New England on grasses growing on extensive sand deposits left by retreating glaciers. The route that it could have taken in crossing the Appalachian Mountains may be traced by present-day sand and gravel deposits (VANR 2011) that represent remnants of moraines (Fig. 12B). Since this spittlebug is unknown from sandy areas in southern NY such as Hempstead Plains, it evidently did not utilize the Hudson Valley to reach the coast. Nor is a more southerly route through OH and PA likely, because sand deposits in OH are discontinuous beyond the middle of the state (USGS 2005), except for those along the shores of Lake Erie, and because the adjacent Alleghany plateau in PA was the first glaciated area to be reforested (Bernabo and Webb 1977). It probably crossed the Appalachians on Little Bluestem growing on sandy soil in low-elevation montane valleys. Residues of moraines in VT are concentrated in the northwestern part of the state around Lake Champlain and form a series of oblique chains across the state to the White River on the eastern watershed (Fig. 12B, red), approximately the route now followed by Interstate 89 across a low divide in the Green Mountains. By contrast, the distribution of *Lepyronia angulifera* clearly shows a postglacial northward migration along the Atlantic coast, then following the Hudson Valley to the Great Lakes (Fig. 5B). This is the same route taken by a sand-inhabiting wasp (Kurczewski 2008).

The overall distribution of the remaining 24 grass-feeding prairie Auchenorrhyncha known so far from the northeastern USA (Figs. 2B, 13) match well with the distribution of drought-prone soils (NRCS USDA 2011). The smallest number of records from New England states are from the Appalachian Mountains, suggesting faunal depletion after erosion decimated sand deposits and deciduous

forests dominated these areas over the last 9000 years (Bernabo and Webb 1977). Thus, sand-adapted prairie grasses and their associated insects, including flightless Cercopidae, must have migrated eastward soon after glaciers retreated and

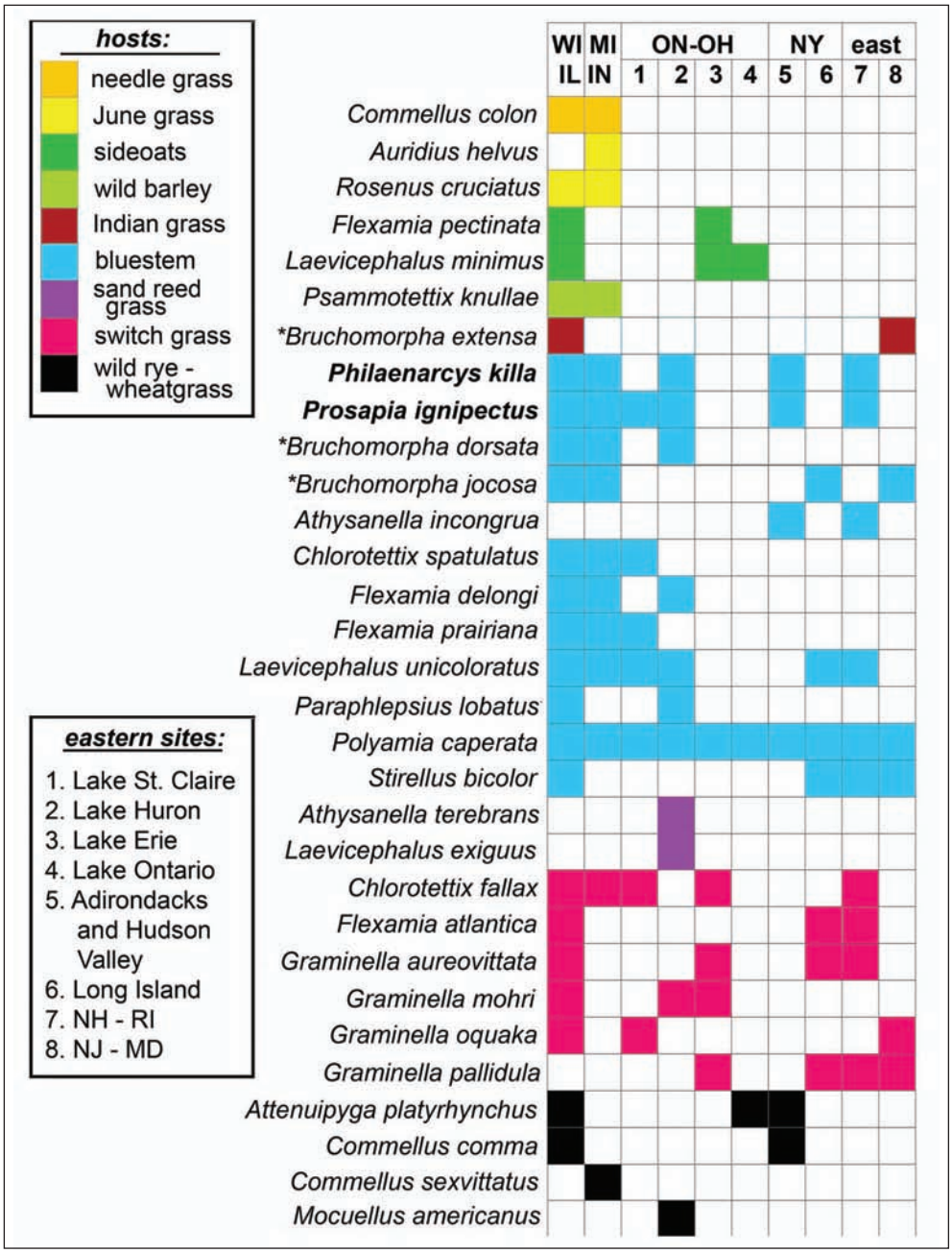


Figure 13. Distribution of 26 northeastern Cicadellidae, 2 Caliscelidae (*) and 2 Cercopidae (boldfaced) specializing on prairie grasses (color key in upper side box) that occur on the "prairie peninsula" (WI–IL / MI–IN) or in glades farther east (ON–MD) with numbered subdivisions specified in lower side box. *Prokelisia crocea* (Delphacidae) is not included in this list, because it is restricted in the east to intertidal grasslands.

before sand deposits were significantly eroded. This reasoning supports the hypothesis that a pre-existing periglacial grassland once extended at least as far east as the longitude of Lake Huron, where there are still 2 endemic segregates of a prairie fauna: *Flexamia huroni* in southern MI and *Laevicephalus exiguus* on the Bruce Peninsula, ON. This biota could have spread across upstate NY (Fig. 14) after the drying up of the Mohawk Valley spillway 11,000 years ago (Rayburn et al. 2003) when herb pollen was on the increase throughout the "prairie peninsula" (Bernabo and Webb 1977).

Pioneer grasses on moraines were probably mostly Switch Grass, which is adapted to unconsolidated sand in disturbed areas. Little Bluestem is a later successional species that could have become dominant throughout the northeast before soils were sufficiently well developed to permit the invasion of trees. The easterly spread of such grasses and their associated insects may have been assisted by dominant westerly winds, dispersing widespread species that are rare in eastern grasslands, such as *Athysanella incongrua*, to sites where they were poorly adapted for survival. The presence of the flightless Sand Plains Spittlebug in most eastern sandy sites suggests that this must have occurred long before the Altithermal period, 8000–6000 years ago, when forests became dominant throughout the New England states. It seems likely, therefore, that most prairie species of grasses and associated insects came to the east from a periglacial source.

The periglacial fauna contrasts with that of Long Island. This difference reflects in part an enrichment of species coming from the south. For example, planthoppers of the genus *Bruchomorpha* (Fig. 7B) include 3 prairie species found across the Gulf and south Atlantic coasts. These indicate their spread

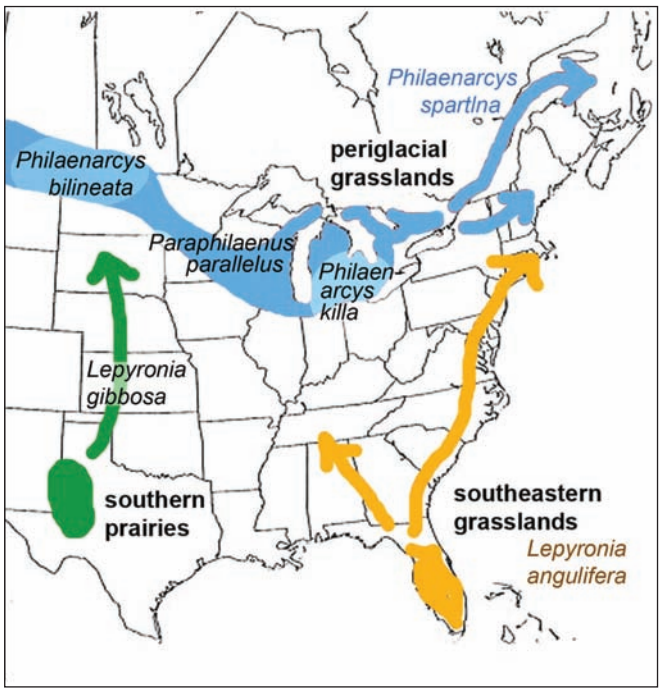


Figure 14. Postulated grassland glacial-age refugia for 6 spittlebugs and their subsequent dispersal patterns (colored names indicate probable glacial disjunct populations from an earlier glacial era).

across the Mississippi River to the southeastern states and subsequent dispersals northwards. The northernmost of these is *B. jocosa*, which is represented in the southeast and as far north as Hempstead Plains by the endemic subspecies *obscura* Ball. Such incursions help create a distinct faunal disjunction between the grassland–pine barrens ecosystem of Long Island and the rest of the New England glades, which are characteristic "heaths".

Conclusions

The data show that the origins of the Great Lakes and Atlantic coastal grasslands biota are complex, and that most of the theories enumerated above contribute something to understanding their biota. Spittlebugs show most clearly the main patterns. The presence of endemic species such as the spittlebugs *Paraphilaenus parallelus* in the Great Lakes region (Fig. 2) and *Philaenarcys spartina* in the Gulf of St. Lawrence (Fig. 5A) are probably derived from periglacial and coastal refugia, respectively, with the latter probably having come during an earlier interglacial period to the Atlantic coast by way of the St. Lawrence Valley. By contrast, *Lepyronia gibbosa* is a widespread prairie species obviously derived from a southwestern refugium and *Lepyronia angulifera* comes to us from a southeastern refugium (Fig. 14). The origins of *Philaenarcys killa* and *Prosapia ignipectus* are more obscure, but probably were likewise associated with a periglacial grassland, taking advantage of grassy passes in the Appalachians soon after glaciers melted. Whether the population of *L. gibbosa* in MA represents a holdover from a previous interglacial time, or whether the specimens were simply mislabeled, must await further study for elucidation.

Agropyron and *Sporobolus heterolepis* from a periglacial flora could have followed saline soils over limestone outcrops to populate alvars around Lake Huron, and Indian Grass could have migrated northwards from the southeastern states soon after deglaciation. Only the role of a sand ecosystem developing on glacial moraines must be added to explain the complexities of the insect fauna on sand-adapted grasses and shrubs. For example, Switch Grass from the southern states could easily have invaded the Atlantic seaboard by way of the exposed offshore banks during lowest sea levels during the glacial period, and as it is a pioneer grass on exposed sand, would have been among the first vegetation to develop on glacial moraines as world temperatures increased towards the end of the ice age.

Thirty Auchenorrhyncha specializing on prairie species in 10 genera of grasses (*Agropyron, Andropogon, Bouteloua, Calamovilfa, Elymus, Hordeum, Koeleria, Schizachyrium, Sporobolus, Stipa*) clearly show a prairie peninsula invasion of glaciated lands east of the Mississippi River, with 7 having spread as far east as the Atlantic coast. A few species, such as the Caribbean *Lepyronia angulifera*, probably went the other direction, migrating up the coast and from there to the Great Lakes region by way of the Hudson Valley, but these did not invade more easterly glades. Two leafhoppers and several Caliscelidae, including an endemic subspecies, probably came from a southern refugium east of the Mississippi River.

The periglacial refugium flora probably included cool-tolerant plants which supported northern species of Auchenorrhyncha: Creeping Juniper, Little Bluestem, Northern Dropseed, Sand Cherry, Sand Reed Grass, and Wheat Grass, with Needle Grass and Wild Barley on well-drained sites, and a mixture of sedges and spikerush with Sandbar Willow occupying low-lying areas prone to spring flooding.

At first, Switch Grass must have become the dominant grass in newly exposed glaciated parts of the east, as it has the largest Auchenorrhyncha fauna in the New England sand plains. The fauna of Switch Grass shows both eastern and western components. *Flexamia atlantica*, which is confined to Switch Grass in open oak woods along the Atlantic coast, may be an Atlantic endemic race biologically differentiated from inland populations, which favor treeless areas. Other Switch Grass specialists of the genus *Graminella* are mostly western, with few eastern populations. This finding suggests that the 6 Auchenorrhyncha specializing on Switch Grass probably rapidly colonized newly exposed sand deposits and may have migrated from both the west and the east, intermixing on the prairie peninsula. However, the distribution of *G. aureovittata* clearly indicates a southeastern refugium for that species and postglacial migration northwards both east and west of the Appalachian Mountains, as predicted by Metzler et al. (2005).

Prairie peninsula grasses in postglacial times formed a distinctive sand plains ecosystem that included calciphiles such as Northern Dropseed and spikerushes only on limestone plains around Lake Huron. Big Bluestem would have been at best a minor component of moraine vegetation, and its only leafhopper specialist, *Flexamia prairiana*, is found eastward only as far as the tip of the prairie peninsula in southern ON (Whitcomb and Hicks 1998). Rapid eastward migration of sand-adapted prairie grasses probably occurred during 9600–9000 MP when lowest Great Lakes water levels would have exposed glacial moraines with great expanses of sand around the Great Lakes. From there, the route by way of valleys in the Appalachian Mountains to the Atlantic coast is more problematic. These dispersal routes are now mostly washed away by postglacial rising lake levels and erosion of the Hudson and Connecticut valleys. Elsewhere, sand and gravel became overlaid with loam that supported the development of forests. However, disjunct Auchenorrhyncha populations and remaining sand and gravel deposits suggest a route across VT rather than down the Hudson River (and from there up the coast to Cape Cod). Sand plains along the lower reaches of the Hudson and Connecticut rivers are glacial-age outwashes from far upstream, and support only the most highly dispersing Auchenorrhyncha, or those that specialize on shrubs such as Sandbar Willow that follow sand-choked streams. The eastern end of Long Island received much outwash sand and probably bluestem seeds from the Hudson Valley, but not any of the northern sand-associated Auchenorrhyncha. It is therefore an extension of southeastern grasslands and bears little relation to the heaths found from RI to ME.

Thus, the subset of 12 Auchenorrhyncha from the study area (Table 2) compared to 30 from the New England states as a whole (Fig. 13) and a total of

62 eastern prairie species (Fig. 8) suggests that the Atlantic sand ecosystem is composite in nature. Grasslands from RI northwards ("heaths") represent the most highly endangered prairie peninsula biota, while those from Long Island southwards have an influx of species from the south. The latter can be divided into "pine barrens" (forest openings maintained by repeated fires) and "plains" (fire-opened grasslands maintained treeless by drought). Presumably, the insect fauna of Long Island pine barrens and plains differs from those of heaths further north because the faunas dispersed at widely separated times. The Hempstead Plains show every indication of having been formed by an extensive burn within the last 400 years on shrubby "pine barrens" fanned by westerly winds, with Switch Grass (a colonizer of exposed sand) initially becoming the dominant tall grass, later superseded by the shorter Little Bluestem, and acquiring their faunas by wind-transported species from pine barrens to the south.

Both "heaths" and "plains" can remain treeless for centuries if covered with a lichen crust. Maintenance of this lichen crust will be needed if there is any hope of retaining these vestiges of the past.

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