



Biodiversity refuges (refugia)

The *Oxford English Dictionary* defines the term *refuge* as a “shelter or protection from danger or trouble.” In a biological context, a refuge represents a habitat, region, or landscape in which populations are able to persist within an otherwise unfavorable landscape. Except for those species that experience an instantaneous, catastrophic, range-wide reduction in population size, most will find final shelter for at least a limited time in some form of refuge before becoming extinct. Others may persist for considerable periods at low numbers in these sites or may expand both population and range size from the refuge to the extent that extinction is no longer likely. It is also common for a suite of rare species to use the same refuge, giving these sites particular importance from a conservation perspective. As a result, understanding the types, scales, and history of refuges—or what biologists term *refugia*—is critical to understanding the dynamics of extinctions and extinction near misses.

The long-term implications of refugia on biodiversity cannot be overestimated. Genetic evidence suggests that during the last full-glacial period, populations of warm-temperate plant and animal taxa were able to persist fewer than 100 miles (a few hundred km) south of the glacial maximum, far north of their presumed main ranges. Species exhibiting this pattern include the European and North American beech, the red maple, the eastern chipmunk, the tiger salamander, and rattlesnakes. The presence of such refugia not only aided biological recovery from rapid Late Pleistocene climate change but also helped increase levels of genetic variability within contemporaneous populations.

What factors distinguish refugia from their surrounding matrix habitats and allow them to be the last places of shelter for endangered species? In general, two main classes of refugia have been identified: environmental and biological. Environmental refugia provide unique climatic/microclimatic, hydrologic, and/or edaphic (soil) conditions not found elsewhere in the surrounding landscape. This category includes habitats that maintain within their confines unique disturbance regimes. Biological refugia represent habitats that protect species from catastrophic predatory, parasitic, epidemiological, and/or competitive interactions with other species. A special class of such refugia consists of nature reserves, which public or private entities have created in an attempt to limit population losses—at least theoretically—by constraining human activities within their boundaries.

Environmental refugia

The maintenance of unique climatic conditions underlies the existence of many refugia. For instance, variance in solar heat transfer stemming from slope angle, orientation, and shading from local vegetation and additional impacts of cold-air drainage leads to almost 10°F (4°C) differences in daily maxima temperatures and more than 5°F (2°C) differences in daily minima temperatures between neighboring microsites in the Great Smoky Mountains National Park of the southeastern United States (Fridley 2009), a region supporting many unique species. This variation is of roughly the same scale (about 12°F or 5°C) as the regional temperature variation between full-glacial to modern times in eastern North America. This impact accounts for the persistence of plant and animal assemblages with lower-temperature and higher-humidity demands on north-facing slopes and higher-temperature and lower-humidity demands on adjacent south-facing slopes. Climatic refugia are also found at larger spatial scales, particularly in mountainous terrain, with higher-elevation sites tending to be much cooler and wetter than low-elevation sites. In the southwestern United States, for instance, mountaintops are often blanketed by Hudsonian spruce-fir forest, whereas low-elevation canyons are often inhabited by Lower Sonoran Desert species.

Not all climatic refugia are associated with topographic variation. Dramatic examples may also be associated with unique geologic conditions. For instance, the warm microclimates immediately adjacent to hot springs and other geothermal features can support populations of species far outside their normal range. Such is the case for populations of the subtropical fern *Adiantum capillus-veneris* along the margin of Fairmont Hot Springs in eastern British Columbia, Canada, which live approximately 1,000 miles (1,600 km) north of the nearest-known colonies in central California. Alternatively, persistent ice reservoirs may develop at the base of open scree slopes far to the south of the typical limits of permafrost. In central Bohemia such sites support isolated populations of high-arctic spiders and mites, whereas in North America sites such as Ice Mountain in eastern West Virginia allow taiga plant and land snail populations to persist hundreds of miles (km) south or 1,000 meters lower than their typical range.

Another important class of environmental refugia is tied to sites that possess unique hydrologic characteristics. For instance, areas of permanent groundwater seepage can allow



Hydrologic refuge on steep, rocky, south-facing slopes near Kamlak in the Altai Republic, Russia. These sites are much drier than the regional mesoclimate, and support species-rich grassland (steppe) vegetation, as opposed to the typical birch/pine forest that otherwise dominates this landscape. Courtesy of Jeffrey C. Nekola.

for the establishment of wetland refugia within very dry landscapes. Exposed permanent aquifers associated with tectonic faults along the western slope of the Ruby Mountains in northern Nevada have created isolated hillside seepages that support a diverse wetland biota consisting of plants, insects, and snails in the Great Basin Desert, where precipitation amounts to fewer than 10 inches (25 cm) per year. Also common are refugia featuring conditions much drier than the surrounding landscape. For this reason sand dunes, limestone pavements, and southwest-facing wind-blown silt (loess) slopes in the central United States often harbor populations of species isolated hundreds of miles from their normal ranges to the south and west.

Perhaps less obvious, but equally important, are refugia characterized by unique edaphic (soil-related) conditions. Pockets of relatively high pH and cation-rich soils in regions characterized by low pH and cation-impoverished conditions often support a large number of extralimital species. This condition is well displayed in isolated cation-rich lava beds in the Piedmont district of the southeastern United States. In comparison with surrounding soils derived from more acid substrata, the soils of these sites are dominated by shrink-swell clays with a cation-exchange capacity that is an order of magnitude greater. As a result, these sites retain a much higher level of soil nutrients and support high-cation-, high-pH-demanding central North American grassland species (e.g., *Silphium terebinthaceum*) within this otherwise hostile landscape. Base-rich conditions associated with anthropogenic shell mounds have allowed numerous plant and land snail species to colonize sites far north of their normal range from the Florida Keys to southeastern Virginia in the southeastern United States. Similar pockets of high-pH and cation-rich soils within the highly acidic northeastern North American taiga support many restricted plant and animal species, including a number that are disjunct from the Western Cordillera region. Conversely, pockets of low-pH and low-cation soils within an otherwise high-pH and cation-rich landscape generate important refugia, as may be observed in the occurrence of multiple southeastern

coastal plain plant and animal species within isolated sand dune sites in central North America.

A final important class of environmental refugia is related to unique disturbance regimes. Sometimes a given disturbance is limited to a given refuge. For instance, in New England and the northern Great Lakes nonforested vegetation patches may be generated through early-spring ice-scour and ice-shove actions along riverbanks and lake shores. Such disturbances maintain numerous populations of rare species that otherwise could not survive in the forested landscape. Along the St. John River in Maine and New Brunswick the endangered *Pedicularis furbishiae* is able to survive only in such sites, while along the northern shores of Lakes Michigan and Huron a multitude of plant and animal species—including isolated populations of the arctic *Selaginella selaginoides* and *Primula mistassinica*—are limited to unforested lake shores.

Additionally, disturbance refugia may be created when sites possess unique return intervals for a given disturbance within a region. The occurrence of isolated old-growth forest communities on the downwind side of water bodies in central North America has often been related to the much longer return intervals for fire in these sites. Such forests support a number of woodland species, such as the Assiniboia Sedge (*Carex assiniboensis*), that are restricted to these sites in this grassland landscape. Furthermore, the existence of isolated open-pine or scrub-dominated hilltops in the dense deciduous forests of the southern Appalachians has frequently been related to much shorter fire-return intervals for these sites because of the increased frequency of lightning strikes. These sites also often support populations of many rare species such as the Mountain Golden Heather (*Hudsonia montana*).

Biological refugia

Sometimes refugia are maintained through the avoidance of negative biological interactions such as competition, predation, parasitism, or disease. Such limitation may be facilitated in two ways: First, the isolation of a refuge from the main range of a potential competitor/predator/disease agent may prevent colonization of these species. In such cases weaker competitors/prey species are given an opportunity to persist. Second, a biological refuge may be created when environmental conditions exclude potential predators/competitors/diseases. An excellent example of this is the persistence of isolated populations outside the natural range of their disease agents. For instance, perhaps the last healthy populations of Fraser fir (*Abies fraseri*) are found in the western Great Lakes region—about 600 miles (1,000 km) outside their natural range—in Christmas tree farms planted beyond the climatic range of the balsam wooly adelgid (*Adelges piceae*), a lethal exotic pest. Similarly, healthy individuals (and sometimes populations) of American chestnut (*Castanea dentata*) persist in isolated US midwestern and northwestern sites that are far outside its natural range and, therefore, have also escaped infestation by *Cryphonectria parasitica*, the fungus that causes chestnut blight. Many of Hawaii's most endangered plants are now limited to almost vertical cliff faces and slopes that are largely immune to grazing by introduced vertebrates such as goats and pigs. These processes are so

important that at large scales the majority of global diversity is apparently related to such “ecological equivalents” that are allowed to exist only because they are kept isolated from superior competitors/predators/diseases (Auerbach and Shmida 1987). In fact, it has been estimated that the bird diversity of Earth would be four times lower if the oceanic barriers between continents were eliminated (Preston 1962).

An important subclass of biological refugia includes sites that have been protected from human depredation because of their isolation or unique disturbance regimes, or through the passage of laws. For instance, the northern elephant seal (*Mirounga angustirostris*) was almost driven to extinction by hunting along the Pacific coast of North America. By the late 1800s, as few as twenty individuals remained and were limited to a single refuge located on Guadalupe Island, 160 miles (250 km) off the Baja California coast. The passage of laws by the United States and Mexico in the early twentieth century prohibiting the hunting of this species has allowed it to recover much of its former range, with the population total exceeding 100,000 by the early twenty-first century. This near brush with extinction, however, created a severe reduction in genetic diversity: surviving populations possess no detectible genetic variation (Bonnell and Selander 1974). In another example, a number of endangered southeastern US pine-wiregrass savanna plants—such as the American chaffseed (*Schwalbea americana*)—are now essentially limited to bombing ranges within military bases where fire-return intervals are maintained at very high levels. Outside these sites this species has disappeared because of fire suppression.

As has been already alluded to, it is important to recognize that these types of refugia are not wholly separate entities. Rather, they represent an interacting suite of components that collectively define the refuge. In most cases a given refuge contains multiple elements from these various categories. For instance, the presence of cooler and moister conditions on a north-facing slope (a climatic factor) will also decrease the return interval for fire (a disturbance factor), with both of these conspiring to generate older and more humid forest communities. In another example, the presence of upwelling groundwater will make a site not only wetter than the surrounding landscape (a hydrologic factor) but also, most likely, more cation-rich (an edaphic factor). Understanding the full range of characteristics defining a given refuge thus requires that all of these factors, and the interactions between them, be well understood.

Refugia scale

Another important aspect of refugia is their spatial scale. Scale plays an important role in determining the body-size range and mobility of the species that are confined to such sites. In general, three size classes have been considered: microscale refugia, which represent single habitat patches often less than 1,000 acres (400 ha) in size; mesoscale refugia, which represent larger unique regions of roughly 1,000 acres to 800 miles² (400 to 200,000 ha); and finally macroscale refugia, which represent entire unique landscapes and encompass more than 800 miles² (less than 200,000 ha).

Microrefugia are perhaps the best known from a biodiversity perspective and represent the many types of unique sites that



An algalic talus slope above Point Hollow Creek at White Pine Hollow State Preserve near New Vienna, Iowa. At this site cold air seepage from subterranean ice deposits creates a climatic microrefuge which maintains late-glacial climatic conditions within an area of less than 1000 m². The rare species limited to this site—primarily rare bryophytes, vascular plants, and land snails—must maintain viable populations within this highly confined space. © Clint Farlinger/Alamy.

have long been known to harbor and maintain rare species populations. Such sites are often the focus for conservation efforts. However, the species able to use these sites tend to be of limited mobility and/or small body size. Thus, microrefugia most often support populations of sedentary species such as vascular plants, bryophytes, fungi, and some invertebrates.

Mesorefugia typically occur in areas supporting unique environmental/biological conditions. Such regions are often associated with prominent geographic features such as shorelines, mountain ranges, or human political divisions. Mesorefugia often include multiple habitat types and may also support populations of larger and more mobile species such as small mammals, birds, and mobile invertebrates. The buffered regional climate associated with areas within 10 miles (15 km) of the Lake Michigan lakeshore represents a classic example of a mesorefugium. The cooler summer temperatures, warmer winter temperatures, and more consistent humidity levels in comparison with that of adjacent inland habitats have allowed the development of a conifer-dominated forest closely resembling the eastern maritime forests of Maine and New Brunswick. This region supports populations of numerous plant and invertebrate species that otherwise do not occur in central North America. For instance, the minute land snail *Planogyra asteriscus*, characteristic of eastern maritime forest, is restricted in central North America to lakeshore forests dominated by the northern white cedar (*Thuja occidentalis*). Another land snail, *Hendersonia occulta*, is a full-glacial relict species that also inhabits these forests. The endangered Hine’s emerald dragonfly (*Somatoblora hineana*) is also largely limited to open wetland sites in this region. Mountain ranges within the Great Basin Desert also are associated with mesoclimates that are cooler and wetter than the characteristic climate of the surrounding landscape. These areas support



Land snails within the genus *Ashmunella* which inhabit the climatic mesorefuges of sky island forests. These pockets of mesic forest are isolated from one another by many miles of intervening lowland desert. Each *Ashmunella* species is restricted to a single sky-island system, as indicated by the mountain listed below each Latin name. Courtesy of Jeffrey C. Nekola.

isolated forest and alpine tundra communities that harbor a large number of species otherwise absent from the landscape, including a number of small mammal (Brown 1971) and land snail species.

Human political divisions with unique laws also represent a type of mesorefugium. For instance, the 350 square-mile (90,000 ha) Menominee Indian Reservation in northeastern Wisconsin has been spared from the forest clear-cutting that is characteristic of the surrounding landscape. Because of this circumstance, the Menominee Reservation is one of the few human political units that is easily identifiable from outer space, and it represents the last relatively intact assemblage of northern mixed-hardwood forest within the landscape. As such, it is an important refuge for many old-growth species.

Macrorefugia develop when entire landscapes possess unique environmental and biological characteristics. Because of the large size of these refugia, species across the entire body-size spectrum may find refuge within their boundaries. For instance, the Altai and Sayan Mountains encompass a region in south-central Siberia some 620 miles by 310 miles (1,000 km by 500 km) that possesses a regional climate very similar to the conditions once found south of the continental ice sheet in western Eurasia during full-glacial times (Horsák et al. 2010). As a result, the small mammal, land snail, and plant communities of this region are almost exact analogs to full-glacial European fossil assemblages. Because of the large size of the region, woolly mammoth (*Mammuthus primigenius*) persisted in the landscape until perhaps 6,000 years ago, whereas the Irish elk (*Megaloceros giganteus*) lasted until 4,000

years ago, during the early Bronze Age. Australia also represents an important macrorefugium, with its isolation from other continental landmasses allowing for the persistence and diversification of a number of unique groups such as marsupial mammals and plants in the Family Proteaceae.

Historical classification

Two additional types of refugia have been recognized based on their relative age in comparison with surrounding matrix habitats. Paleorefugia represent habitats that are older than the surrounding landscapes, whereas neorefugia represent habitats that are younger (Nekola 1999). As these terms reflect the age of a given refuge relative to its surroundings, a paleorefugium in one landscape may be of more recent origin than a neorefugium in another. It is also possible that a particular habitat type that developed as a paleorefugium in one landscape may be a neorefugium elsewhere.

The relative importance of extinction and immigration varies greatly between paleorefugia and neorefugia. First, consider the development of paleorefuge sites. Before environmental change, a given habitat might be continuous over a wide geographic extent, harboring a diverse and well-mixed biota potentially near equilibrium with the environment. Following environmental change, the habitat may become restricted to a few discrete patches in the landscape. As this community becomes fragmented, habitat size decreases and isolation between fragments increases, leading to increased extinction rates. Individual site richness will fall, with larger fragments retaining more taxa than smaller ones. Although



The Altai Mountains in southern Siberia represent a climatic macrorefuge which maintain full-glacial climatic conditions across a large landscape. The flora and fauna of this region is essentially identical to Wisconsinan full-glacial fossil assemblages found in central and western Europe. This region was the last area on the Eurasian continent to support mammoth and Irish elk populations. © Maxim Toporskiy/Alamy.

some recolonization from nearby sites undoubtedly occurs, this should not greatly influence the large-scale compositional pattern as nearby sites should have been originally colonized from similar species pools.

In contrast, neorefuge sites are created through the development of novel environmental conditions in a landscape (compare time periods *B* and *C* in Figure 1). Consequently, the biota of neorefugia must be a product of immigration. Factors that affect immigration, such as habitat isolation or age, should therefore exert a greater influence on community composition and species richness. Although extinction certainly occurs in these sites as newly recruited populations disappear, this process should be of limited importance because populations can become extinct only if a successful immigration has previously occurred and because incomplete dispersal between sites should lead to low rates of competitive exclusion.

Such differences in the relative contribution of extinction and immigration have been empirically documented for various insular habitats. For instance, the species richness of land-bridge islands (paleorefugia) is primarily determined by extinction rates. Extinction is also the principle process that has shaped rodent faunas of Great Basin montane alpine communities (paleorefugia), which became fragmented following the

close of Wisconsinan glaciation. The importance of immigration in the development of young volcanic island biotas (neorefugia) has been shown on the islands of Krakatau, Long, and Ritter in the eastern Pacific. Similar patterns were

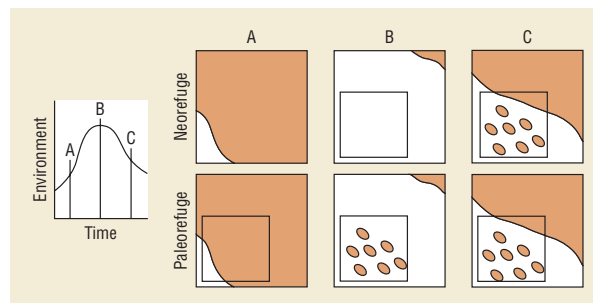


Figure 1. Diagrammatic representation development paleorefugia and neorefugia development. At time period *A*, environmental conditions favor a particular habitat (shaded). After critical environmental change (time period *B*), this habitat has retreated completely from the focal landscape (inner box) in the case of neorefugia but persists as isolated patches in the case of paleorefugia. By time period *C*, the environment has changed again, allowing the habitat to exist again within portions of its original range. Reproduced by permission of Gale, a part of Cengage Learning.

demonstrated in manipulative experiments on mangrove islands off the South Florida coast.

The differential importance of extinction versus immigration leads to significant differences in the way that paleoregion and neoregion communities are structured. A comparison of paleoregion sites (algific talus slopes) to neoregion sites (fens) within the same landscape in northeastern Iowa documents the following four points.

1. Relationships between species and area are steeper and stronger in paleoregion than in neoregion. While both habitats demonstrate a significant positive relationship between species richness and habitat size, both slope and intercept for algific talus slopes are significantly ($\rho = 0.000$) larger than those reported for fens. As a result, small algific talus slopes support fewer vascular plant species than fens of identical size, whereas large algific talus slopes have greater species richness than fens of identical size. The amount of variance explained in these regressions also differ greatly. Log-transformed habitat size accounts for 32.6 percent of observed variance in algific talus slope species richness, but only 6.3 percent of the variance in fen species richness. This difference was found to be highly significant ($\rho = 0.006$).
2. The relationships between species and habitat isolation are stronger in neoregion than in paleoregion. Habitat isolation is a significant additional predictor of vascular plant species richness in fens for all isolation index values (ρ -values ranging from 0.003 to 0.027), with the amount of additional variance explained by habitat isolation being roughly the same as that explained by habitat size. For algific talus slopes, however, habitat isolation was never a significant additional predictor of species richness (ρ -values ranging between 0.150 and 0.802).
3. Distance decay patterns are more pronounced in neoregion than in paleoregion. In fens, significant ($\rho = 0.0001$) decay in compositional similarity with increasing geographic distance is apparent at all sample grain sizes, accounting for over one-third of observed variance among regions 50 miles by 50 miles (80 km by 80 km) in size. In algific talus slopes, the distance decay was not a significant predictor of species composition at any scale.
4. The dispersal strategies of species vary between paleoregion and neoregion. The frequencies of various dispersal classes differed significantly ($\rho < 0.0005$) between the two habitats. Species with berries, fleshy fruits, or nuts were approximately 15 times more frequent in algific talus slopes than in fens, whereas species with plumose seeds were approximately 7 times more frequent in fens than in algific talus slopes (see Table 1).

These analyses suggest that paleoregion are more biotically self-contained than neoregion, with immigration playing a relatively minor role in the determination of species occurrence. The protection of the biota of such habitats should thus center on those sites that harbor maximum diversity and on the internal site

Habitat	Dispersal class			
	1	2	3	4
Algific slope	26 (51.0%)	10 (19.6%)	13 (25.4%)	2 (3.9%)
Fen	42 (52.5%)	1 (1.2%)	17 (21.3%)	20 (25.0%)

Log-likelihood chi-square: 20.998 $P < 0.00005$

- 1 = Macroscopic, non-plumose seeds in dry capsules
- 2 = Berries/nuts
- 3 = Microscopic seeds/spores
- 4 = Plumose seeds

Table 1: Frequency of four dispersal classes among restricted vascular-plant species in northeastern Iowa fen and algific slopes. The numbers in parentheses represent the percentage of the total number of species recorded in each habitat contained in each dispersal class. Reproduced by permission of Gale, a part of Cengage Learning.

dynamics that are responsible for that diversity. However, these analyses also suggest that neoregion are not as self-contained, with immigration from surrounding sites strongly influencing biotic composition. The species richness in these communities varies conversely with habitat isolation, with community composition being strongly influenced by proximity of source areas. Adequate protection of neoregion biodiversity thus includes not only the protection of internal site dynamics but also the immigration potential between sites. Such protection will be possible only if many sites are protected across the landscape, including those that may not currently support diverse biotas. Consequently, neoregion reserve design requires an integrated, regional strategy.

Biological refugia in the real world

To help make these concepts more concrete, three different biological refugia from North America are detailed. Two of these are found in northeastern Iowa: algific talus slopes represent a climatic refugia, whereas spring fens represent a hydrological refugia. Although both are micro-refugia, with habitat sizes never exceeding 1,000 acres (405 ha), algific slopes represent a paleoregion, whereas fens represent a neoregion. In addition, Madran Sky Islands from the desert southwest are also described: These represent meso-scale climatic paleoregions.

Algific talus slopes are characterized by a unique buffered microclimate created through the constant issue of cold, humid air from associated ice caves. Their soil temperatures rarely exceed 60°F (15°C) in the summer and are not as cold in the winter as surrounding forest habitats. Approximately 300 algific talus slope sites have been located across a ten-county region of northeastern Iowa in exposures of Prairie du Chien, Galena, Blanding, or Hopkinton Formation carbonates (see Figure 2). A limited number of sites are also known from adjacent portions of Minnesota, Wisconsin, and Illinois.

Algific talus slopes occur within a deciduous forest matrix on steep, usually north-facing, carbonate talus slopes associated with ice caves that developed through ice wedging during the Wisconsinan. Those karst systems that were protected from climatic warming by overlying rock units, accumulated talus

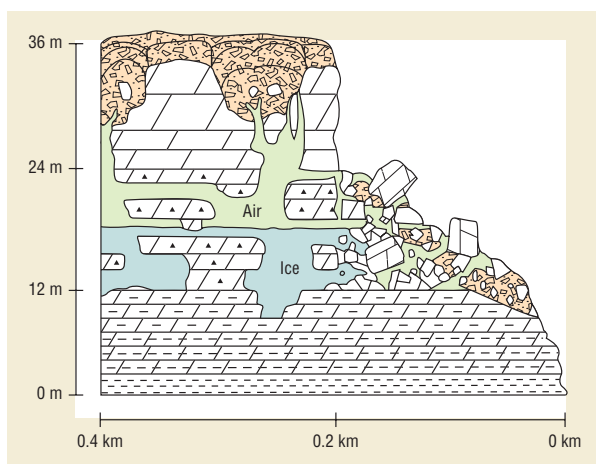


Figure 2. Cross-section view of a Blanding Formation algific talus slope showing major geomorphological features. A complete system has small sinks in the forested upland; vertical mechanical karst fissures in the Hopkington Formation; ice reservoirs in mostly horizontal mechanical karst in the thin-bedded Blanding Formation; underlying relatively impervious Tete des Mortes, Mosalem, and/or Maquoketa formations. (Modified from Nekola 1999.) Reproduced by permission of Gale, a part of Cengage Learning.

debris over cave entrances, and/or a north-facing aspect have been able to retain a below-freezing mean annual temperature.

Algific talus slope habitats range from densely forested to moderately open. Characteristic woody species include *Acer saccharum*, *Acer spicatum*, *Aibes balsamea*, *Betula lutea*, *Betula papyrifera*, *Fraxinus americana*, *Juglans cinerea*, *Pinus strobus*, *Salix bebbiana*, *Sambucus pubens*, *Taxus canadensis*, and *Tilia americana*. The ground layer is typically dominated by a dense bryophyte cover, which supports large populations of pteridophytes such as *Cystopteris fragilis*, *Gymnocarpium robertianum*, and *Equisetum scirpoides*. Woody plant cover decreases and bryophyte/pteridophyte cover increases in general with increasing intensity of cold-air seepage. Algific talus slopes harbor populations of over sixty vascular plant species that are isolated in Iowa from wet taiga and bog forests, including *Adoxa moschatellina*, *Carex media*, *Cornus canadensis*, *Linnaea borealis*, *Mertensia paniculata*, *Poa paludigena*, *Pyrola asarifolia*, *Rhamnus alnifolia*, *Ribes hudsonianum*, *Streptopus roseus*, and *Viola renifolia*. At least three plant species are almost completely restricted to these sites (*Aconitum noveboracense*, *Chrysosplenium iowense*, and *Sullivantia renifolia*). Algific talus slopes also harbor populations of a number of disjunct bryophyte species, including *Rhytidiadelphus triquetrus* and *Seligeria pusilla*. At least eight land snail taxa that were thought to have become extinct at the end of the Wisconsinan also occur on these sites, including the endangered Iowa Pleistocene snail (*Discus macdimockii*). Relict mites in the family Rhagidiidae and Collembola also occur on algific talus slopes.

These taxa were components of a full-glacial community associated with quasi-maritime climates found immediately south of the continental ice margin. The populations became restricted to algific talus slopes when this climatic regime disappeared following the retreat of glacial ice from the continental interior. Because of the intense microclimatic buffering provided by

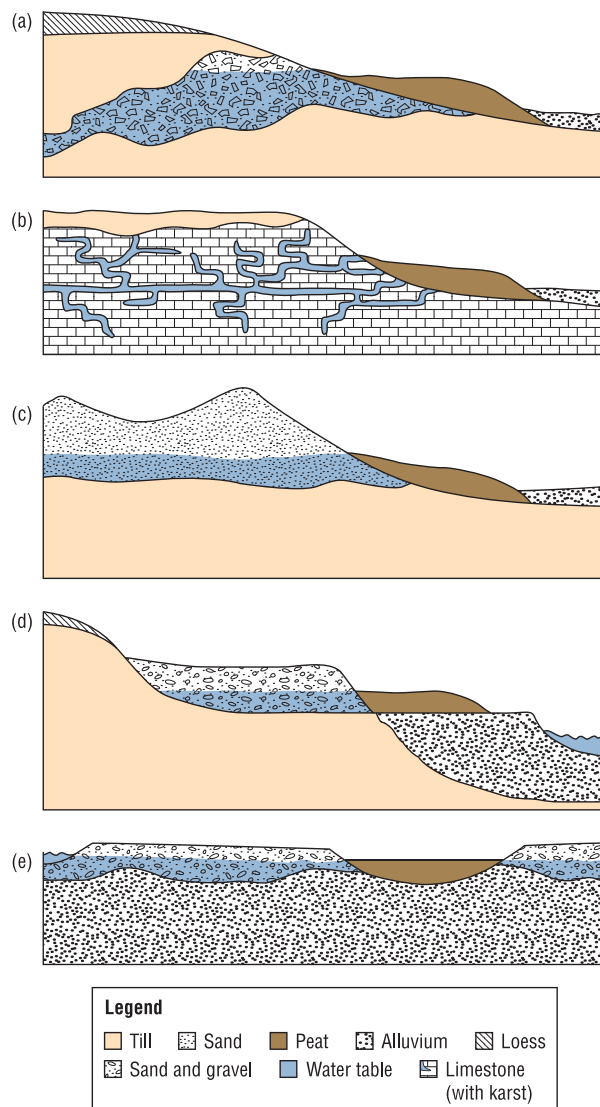


Figure 3. Cross section of the five geologic features that give rise to fen formation in northeastern Iowa: (a) pre-Illinoian till sites, with groundwater seepage from sand and gravel lenses interbedded between till units; (b) bedrock sites, with groundwater seepage from fractured rock; (c) aeolian sand dune sites, with groundwater seepage from dune base; (d) fluvial sand sites, with groundwater seepage from fluvial or outwash terrace bases; and (e) oxbow sites occupying cutoff stream channels. (Modified from Nekola 1999.) Reproduced by permission of Gale, a part of Cengage Learning.

cold air seepage, populations have persisted on algific talus slopes through maximum global warming from about 8,000 to 6,000 years ago to the cooler and wetter conditions of modern times. Algific talus slopes thus represent paleorefugia with biota predating that of the surrounding deciduous forest matrix.

Spring fens represent confined peatland habitats that are fed by underground—rather than surface—water sources. Occurring

in many landscapes, fens are so common in many northern locations that they become part of the biotic matrix and cannot be considered refugia. In places such as central North America, however, fens are rare and possess a hydrologic regime quite distinct from the surrounding tallgrass prairie. In northeastern Iowa, fens are scattered across a thirty-county region where 2,333 sites occurred as recently as the mid-1900s and where only 160 remained extant as of 1990. The bulk of presettlement and extant fens are found on the Iowan Erosional Surface, which was formed during the Wisconsinan through intense permafrost erosion, which removed older tills, created a stepped landscape surface, and prevented the accumulation of deep loess deposits. Similar fen habitats are known in northwestern Iowa, Illinois, Minnesota, Kansas, Nebraska, South Dakota, and Wisconsin.

In northeastern Iowa, fens develop at places of local groundwater discharge from pre-Illinoian tills, bedrock, aeolian sands, fluvial sands, or oxbow-meander cutoffs (see Figure 3). Sites typically occur as hillside terraces or more rarely as flat expanses in low swales or as mounds fewer than 15 feet (4.5 m) tall. The constant issue of groundwater at fen sites creates a buffered habitat somewhat similar to algific talus slopes, possessing more constant soil moisture and soil temperatures being cooler in the summer and warmer in the winter than is characteristic of the surrounding landscape.

In northeastern Iowa, fen habitats are dominated by a dense sedge turf that includes *Carex buxbaumii*, *C. interior*, *C. lanuginosa*, *C. lasiocarpa*, *C. prairea*, *C. stricta*, *C. suberecta*, and *C. tetanica*. In water discharge zones, *Scirpus validus*, *Typha angustifolia*, and *T. latifolia* often become dominant. Scattered clumps of low shrubs are also frequent. These include *Cornus stolonifera*, *Salix bebbiana*, *S. discolor*, *S. petiolaris*, and *S. rigida*. In areas of highest soil saturation, vascular plant growth often becomes stunted and sparse, with bryophytes becoming dominant. Approximately 50 percent of the vascular plant species of these sites are regionally rare. More than 80 of these species are disjunct from open peatlands in boreal or northeastern North American, including *Aster junciformis*, *Betula pumila*, *Carex sterilis*, *Epilobium strictum*, *Eriophorum angustifolium*, *Galium labradoricum*, *Gentiana procera*, *Lobelia kalmii*, *Menyanthes trifoliata*, *Mimulus glabratus* var. *fremontii*, *Parnassia glauca*, *Rhynchospora capillacea*, *Salix candida*, *Salix*

pedicellaris, *Solidago uliginosa*, *Triglochin maritimum*, and *T. palustris*. Northeastern Iowa fens also harbor populations of a number of regionally rare bryophyte, butterfly and skipper, and land snail species.

Carbon¹⁴ dates of basal peat layers indicate that northeastern Iowa fens initiated peat development following the end of maximum global warming, less than 6,000 years ago. Although a few sites possess basal peat dates extending to 10,000 years ago, the presence of oxidized layers within these beds indicates that deposition was not continuous and that at some point even these sites dried out. Thus, while fens may have occurred at modern locations in the late-glacial landscape, the geological record indicates that they have not maintained continuous environmental buffering. Because of this, isolated populations of boreal taxa occurring within these sites cannot represent Late Pleistocene or Early Holocene relicts but are instead relatively recent immigrants into the landscape. In northeastern Iowa, therefore, fens represent neorefugia that are younger than the surrounding tallgrass prairie.

Isolated mountain ranges in the southwestern United States and northern Mexico are large and high enough to generate cooler and wetter mesoclimates in comparison with the climates of the surrounding grasslands and scrublands of the Sonoran and Chihuahuan deserts. As a result, forest communities are able to develop in these high-elevation sites. The forests of the Madrean Sky Islands represent the second-highest center for plant endemism between the Pacific coast and the Great Plains, with perhaps 60 percent of all species being endemic to the region. Additionally, these forests support a wide array of endemic land snails and many other invertebrate taxa. While it has generally been assumed that mesic forest habitats and populations were able to coalesce during the full glacial maximum, paleoecological analyses suggest that such simple models of biome displacement are insufficient to explain the levels of genetic differentiation between populations. It thus appears likely that these refugia were persistent across much of the Pleistocene, making them examples of mesoscale paleorefugia that maintain biotic elements from the former arcto-Tertiary forest.

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