Chapter 8

Lichens and allied fungi of the Atlantic Maritime Ecozone

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Abstract: About 890 species of lichen-forming fungi and more than 30 species of calicioid fungi in the Mycocaliciales are known in the Atlantic Maritime Ecozone of eastern Canada. Based on comparisons with better-studied European lichen biotas, it is estimated that about 25% of the species occurring in the ecozone have yet to be documented. Lichenicolous fungi other than calicioid species remain poorly known, and there has been little focus on the algal and cyanobacterial components of lichen diversity. The historical and global contexts of the biota are reviewed, and patterns of disjunction noted. Climatic variation and associated vegetation gradients across the ecozone are described, and a preliminary categorization is provided of patterns of lichen distribution within this context. It is concluded that the ranges of lichens in the Atlantic Maritime Ecozone are more nearly in a state of equilibrium with prevailing climatic conditions than are those of vascular plants. The rarity of adventive species is inferred to be mainly a consequence of the efficient past and present dispersal of most lichens. While considerable scope remains for increasing knowledge of diversity and distributions, there is also a need for research on the community structure and composition, habitat and substrate ecology, life histories, and most urgently, the conservation of the lichen biota. The Atlantic Maritime Ecozone is an important refuge for many lichens that have undergone sharp declines in neighbouring regions, owing to habitat loss, air pollution, and other human impacts.

Résumé : Environ 890 espèces de champignons formant des lichens et plus de 30 espèces de champignons calicioides de l’ordre des Mycocaliciales sont connues dans l’écozone maritime de l’Atlantique de l’est du Canada. D’après des comparaisons avec des biotopes de lichens européens mieux étudiés, il est estimé qu’environ 25 % des espèces présentes dans l’écozone n’ont pas encore été documentées. Les champignons lichénicoles, autres que les espèces calicioides, restent mal connus, et les composants algaux et cyanobactériens des diversités de lichens ont été peu étudiés. Les contextes historique et global du biotope sont étudiés, et des modèles de disjonction sont dégagés. La variation climatique et les gradients de végétation associés dans toute l’écozone sont décrits, et une catégorisation préliminaire de la répartition géographique des lichens est établie dans ce contexte. Il en ressort que les catégories de lichens présentes dans l’écozone maritime de l’Atlantique sont plus près d’un état d’équilibre dans les conditions climatiques dominantes que celles des plantes vasculaires. La rareté des espèces adventices est inférée comme étant principalement une conséquence de la dispersion efficace passée et présente de la plupart des lichens. Alors qu’un champ d’application considérable demeure ouvert à l’accroissement de la connaissance de la diversité et de la répartition des espèces, il existe également un besoin de recherches sur la structure et la composition des communautés, l’écologie de l’habitat et du substrat, les cycles biologiques et, de façon prioritaire, la conservation des biotopes de lichens. L’écozone maritime de l’Atlantique est un refuge important pour de nombreux lichens qui ont subi un net recul dans les régions voisines, en raison de la perte de leur habitat, de la pollution atmosphérique et d’autres anthropisations.

Introduction

Lichens contribute substantially to the biodiversity and functioning of terrestrial ecosystems throughout the Atlantic Maritime Ecozone (AME), a region covering the eastern Canadian provinces of New Brunswick, Nova Scotia, and Prince Edward Island, as well as Îles de la Madeleine, part of the the Eastern Townships, and the Gaspé region of Quebec. On its rocky shores, they extend into marine and freshwater environments. They are most conspicuous on tree trunks and branches, snags, open rocky outcrops, and other substrata on which few other organisms are able to gain a foothold. Some compete successfully with vascular plants and bryophytes in the ground layer of dry forest openings, sandy or rocky heathlands, and peatlands. As a group, their comparative success in these situations rests in large part on their means of obtaining water, and enduring drought.

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As poikilohydric systems, lichen thalli absorb water directly from precipitation, fog, or dew, as well as from their substrata. They are also able to take up water vapour from unsaturated air during periods of high relative humidity (>75%) and cool temperature (< c. 20°C) (Nash 1996). While those with cyanobacterial symbionts require wetting with liquid water to activate photosynthesis, green algal lichens can attain photosynthetic rates up to 50% of maximum values when they are hydrated by water vapour alone (Lange et al. 1986; Büdel 2007). This enables some to colonize highly xeric substrata in otherwise humid habitats. Among these are, for example, lichens occurring in old-growth forests on dead, decorticated wood, or portions of tree trunks shielded from rainfall, drip, or stemflow. But to varying degrees, lichens also tolerate and indeed require desiccation. Cyclic drying and wetting favours the coordinated development and growth of their photosynthetic (“photobiont”) and fungal (“mycobiont”) partners. Continuous saturation or high humidity is inimical to the majority of lichens not specially adapted to growing in wet conditions.

As they dry out, lichen thalli approach a state of physiological dormancy (Honegger 1998). Membranes and other cellular components and processes are protected by high concentrations of soluble, photobiont-derived sugar alcohols (polylols) or polyamines (Nash 1996). Lichens occurring in exposed, sunny habitats are thereby able to survive episodes or extended periods of high light and high temperature that would induce lethal rates of respiration in hydrated thalli (Kershaw 1985). A range of pigments and other compounds deposited in their cortical layers confer protection against ultraviolet radiation in such situations. The forms and colouration of lichens (Fig. 1A–F) thus embody evolutionary trade-offs, facilitating wetting and drying, and optimal illumination of their photobionts.

During winter in the AME, lichens growing on trees or other substrata projecting above the snow are regularly exposed to minimum temperatures of −15 to −25°C. Their tolerance of freezing and freeze–thaw episodes is linked to their tolerance of desiccation (Nash 1996). Ice nucleation in lichen thalli occurs on the exterior surfaces of the fungal hyphae, withdrawing water from the cells of both partners and increasing intracellular polylol concentrations. The resulting shrinkage of cells and, in the mycobiont, formation of cytoplasmic gas bubbles (cavitation) are reversible upon rehydration (Honegger 1998).

Like mycorrhizas and mycorrhizal fungi, lichens and lichen-forming fungi are biological, not taxonomic groups. The genus and species names by which lichens are conventionally designated refer to their fungal partners, and also serve as a shorthand for the fungal–algal/cyanobacterial symbiosis. All but a small number of the approximately 17 000 currently recognized species of lichen-forming fungi are ascomycetes (Feuerer and Hawksworth 2007). Fewer than 50 lichen-forming basidiomycetes are known, and of these, four have been found in the AME: *Lichenomphalia hudsoniana* (H.S. Jenn) Redhead et al., *L. umbellifera* (L.) Redhead et al., *Multiclavula mucida* (Pers.) Petersen, and *M. vernalis* (Schw.) Petersen. (Nomenclature throughout this chapter follows Esslinger (2008).) *Lichenomphalia* species form a small clade, lichenized with the green alga *Coccomyxa*, that arose within the otherwise non-lichenized, mushroom-forming genus *Omphalina* in the Hygrodiaceae (Redhead et al. 2002; Matheny et al. 2006). *Lichenomphalia umbellifera* forms dark green granular crusts on rotting wood and peat in cool, moist, coniferous forests along the Fundy and Atlantic coasts; *L. hudsoniana* occurs on similar substrata, but forms neatly delimited pale grey–green squamules. It is more exclusively boreal in distribution, so far known in the ecozone only from the highlands of Cape Breton Island and Gaspésie. *Multiclavula* species are part of a morphologically diverse clade, including the chanterelle mushrooms and other “cantharelloid” fungi (Moncalvo et al. 2006). They form small, erect, club-like basidiomata. Although associated with *Coccomyxa*, they lack a well-organized thallus. The status of these associations as lichens is therefore debatable.

In recent years, studies of DNA sequence–variation have yielded a vast array of new characters supporting reconstruction of the evolutionary history of lichen-forming ascomycetes. There have been multiple origins of lichen symbioses among these fungi (Schoch et al. 2009). Reversions to a non-lichenized state have also occurred in various ancestrally lichenized fungal lineages. Together with reassessments of morphological characters, molecular phylogenetic studies are contributing to profound changes in the higher-level classification of lichen fungi, resulting in more natural groupings. Much of this ongoing work has been accomplished through the “Assembling the Fungal Tree of Life” (AFTOL) project (Lutzoni et al. 2004; Spatafora et al. 2006). All currently recognized classes and orders of ascomycetes known to include lichen-forming species are represented in the lichen biota of the AME (Table 1). Consistent with the global distribution of lichenization among these groups, the most species-rich class in the ecozone is by far the Lecanoromycetes, comprising >90% of the biota.

In about 10% of lichens, globally and in the AME, the photosynthetic partner is a cyanobacterium. *Nostoc* is the most common of these “blue–green” photobionts. *Stigonema, Scytonea, Gloeocapsa, and Calothrix* are also represented among the cyanolichens occurring in the ecozone. Cyanolichen diversity on the fungal side is concentrated in the Peltigerales, which includes many conspicuous macrolichens, some of them three-part symbioses. In these, a green alga is the primary photobiont, but *Nostoc* is also present, generally inducing the formation of discrete structures termed cephalodia (Fig. 1A). In a few cases, a single fungal species can form separate, morphologically contrasting thalli with either green or blue–green photobionts. This phenomenon is rare in the AME, so far documented only in *Lobaria quercizans* Mich. and *Peltigera aphthosa* (L.) Wild. The selectivity of cyanolichen-forming fungi for particular *Nostoc* strains is variable. It is low in several *Peltigera* species (O’Brien et al. 2005), but cases of high selectivity are possibly more frequent (e.g., Myllys et al. 2007).

Green algal photobionts belong to two major, distantly related classes: Trebouxiophyceae and Ulvophyceae (Friedl and Bhattacharya 2002; Prösschild and Leliaert 2007). In gen-
**Fig. 1.** Examples of lichens occurring in the Atlantic Maritime Ecozone (AME). (A) *Peltigera aphthosa*. The cortex of the leaf-like thallus becomes translucent when wetted, revealing a continuous underlying layer of green algae (*Coccomyxa* sp.). Nitrogen-fixing cyanobacteria (*Nostoc* sp.) are localized in tiny freckle-like “cephalodia”. The thallus lobes are upturned, exposing the white-edged, non-corticate lower surface. (B) *Cladonia rappii*. The upright portion of the thallus is a hollow “podetium” consisting of regular tiers of stalked cups. Each tier represents a year’s growth. The form of the podetium varies widely among the more than 70 species of *Cladonia* occurring in the AME. (C) *Xanthoria elegans*. The orange cortical pigment protects the photobiont from damage by high light levels. *Xanthoria* and *Caloplaca* have traditionally been distinguished on the basis of their growth forms: foliose in the former, crustose in the latter. But recent studies show that the form of the thallus is not a reliable indicator of phylogenetic relationships within this group of lichen fungi. (D) *Usnea trichodea*. The original description of *U. trichodea* in 1803 was based on a specimen collected in Nova Scotia (see main text). *Usnea* species are most abundant in habitats with high light levels and high relative humidity. (E) *Rhizocarpon lecanorinum*. Each yellow-pigmented “areole” present on this rock-face is <1 mm in diameter. Each stems from a separate instance of reassociation of a germinated ascospore and a cell or cells of a compatible green photobiont. A fringe (“prothallus”) of dark-pigmented fungal hyphae surrounds each areole. (F) *Thamnolia subuliformis* (*T. vermicularis* var. *subuliformis*). The prostrate white podetia, here growing among the flowering plant *Diapensia lapponica*, have never been found with sexual reproductive structures. Molecular phylogenies place *Thamnolia* in a clade including the common “pink earth lichen” (*Dibaeis baeomyces*). *Thamnolia* occurs throughout the world in arctic, antarctic, and alpine environments. In the AME, it is known only from the plateau of the Chic-Choc Mountains in Gaspésie.
general, lichen fungi show strong specificity at the level of orders, classes, and sometimes families, genera, or species, for these algal classes and particular clades (e.g., genera or species) within them (Rambold et al. 1998; Piercey-Normore and DePriest 2001; Miadlikowska et al. 2006). For example, Arthoniales and Ostropales (see Table 1) are lichenized mainly with Trebouxia and Asterochloris species (Trebouxia s.l.) are the most common lichen photobionts, particularly in association with several orders of Lecanoromycetes. Other trebouxiphycean genera represented among the lichens of the AME include Coccomyxa, Dictyochloropsis, Elliptochloris, Myrmezia, and Stichococcus (see Friedl and Büdel 1996). There are surprisingly few reports of free-living Trebouxia populations, though this may be mainly a reflection of the dearth of targeted searches at appropriate scales (Sanders 2005). Trebouxia species are widely dispersed via soredia and other types of joint fungal–algal propagules. The existence of extensive free-living populations can be inferred from population genetic studies (e.g., Yahr et al. 2006) and from the life histories of lichens lacking such propagules (e.g., Beck et al. 1998; Clayden 1998; see also Fig. 1E). The selectivity of a given lichen fungus for various compatible Trebouxia photobionts can vary across ecological gradients and geographic regions (Piercey-Normore 2004, 2006; Yahr et al. 2006). Conversely, particular Trebouxia genotypes can be shared among numerous, closely to distantly related lichen fungi (Piercey-Normore and DePriest 2001). In their diverse habitats and communities, various lichens may thus form ecological guilds, drawing on pools of shared photobionts (Rikkinen 2003).

**Scope and lichenological exploration of the ecozone**

The AME takes in the Maritime Provinces, the Îles de la Madeleine, and the montane Appalachian region of Quebec, east and south of the St. Lawrence River valley (Ecological Stratification Working Group 1995). This broad delineation reflects the small scale of ecozone mapping (1:7 500 000), a high level of ecological generalization, and weighting of phys-

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**Table 1. Classes, orders, and selected genera of Ascomycota represented by lichen-forming species in the Atlantic Maritime Ecozone.**

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
<th>Genus</th>
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<tr>
<td>Lichinomycetes</td>
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<tr>
<td>Arthoniales</td>
<td>Arthonia, Arthrothelium, Bactrospora, Chrysothrix, Cresponea, Lecanactis, Opegrapha, Schismatoma</td>
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<tr>
<td>Dothideomycetes</td>
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<td>Capnodiales</td>
<td>Racodium</td>
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<tr>
<td>Order uncertain</td>
<td>Antisomerdium, Collemopsidium, Trypethelium</td>
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<tr>
<td>Eurotiomycetes</td>
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<tr>
<td>Pyrenulae</td>
<td>Pyrenula, Strigula</td>
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<tr>
<td>Verrucariae</td>
<td>Dermatocarpon, Polyblastia, Staurothele, Verrucaria</td>
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<tr>
<td>Mycocaliciales</td>
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<td>Lichenomycetes</td>
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<td>Lichinae</td>
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<td>Lecanoromycetes</td>
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<td>Acarosporales</td>
<td>Acarospora, Polysporina, Sarcogyne</td>
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<td>Candelariae</td>
<td>Candelaria, Candelariella</td>
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<td>Pertusariae</td>
<td>Aspicilia, Dibaeis, Icmadophila, Ochrolechia, Pertusaria, Thammalia</td>
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<tr>
<td>Baeomycetales</td>
<td>Baeomyces</td>
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<tr>
<td>Agryrales</td>
<td>Placyniella, Rimularia, Schauereria, Trapelia, Trapeliopsis, Xylographa</td>
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<tr>
<td>Ostropales s.l.</td>
<td>Coenogonium, Diploscihes, Graphis, Gylecta, Loxospora, Phlyctis, Stictis, Thelotrema</td>
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<td>Umbilicariales</td>
<td>Fuscidea, Hypocenomyce, Lasallia, Ophioparma, Umbilicaria</td>
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<tr>
<td>“Rhizocarpales”</td>
<td>Catolechia, Rhizocarpon</td>
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<tr>
<td>Lecideae</td>
<td>Amygdalaria, Lecidea, Lecidoma, Porpidia</td>
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<tr>
<td>Pelitgerae</td>
<td>Colleme, Degelia, Erioderma, Fuscopannaria, Leptogium, Lobaria, Maxsalongia, Moelleropsis, Nephrum, Pannaria, Parmeliella, Peltigera, Placyniium, Protopannaria, Pseudocyphellaria, P soroma, Solorina, Sticta</td>
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<td>Teloschistales</td>
<td>Anaptychya, Buellia, Calicum, Caloplaca, Dimelaena, Heteroderma, Megalospora, Phaeospscia, Physcia, Physcionia, Pyxine, Rinodina, Xanthoria</td>
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<tr>
<td>Lecanorales</td>
<td>Ahtiana, Alectoria, Anzia, Bacidia, Biaota, Bryoria, Cetraria, Cetrelia, Cladotria, Cladotria, Eternia, Hypogymnia, Lecanora, Lecidelia, Lepraria, Melanelia, Melanelixia, Melanohalea, Mycoblastus, Parmelia, Platismatia, Punctelia, Ramalina, Sphaerophorus, Stereocaulon, Tuckermanopsis, Usnea, Valpicida</td>
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Species Diversity in the Atlantic Maritime Ecozone
The large indentation between Quebec and the Maritime portion of the ecozone is an artefact of national political boundaries. Much of the state of Maine would otherwise be included. On the other hand, the boreal uplands of northern New Brunswick and Gaspésie are effectively outliers of the Boreal Shield Ecozone. They were evidently mapped within the AME, as, physiographically, Gaspésie is part of the Appalachians not the Canadian (Laurentian, Precambrian) Shield. With the inclusion of Gaspésie, the ecozone encompasses a wide range of bioclimates, described more fully below.

The history of investigation of the lichen biota of Canada has been summarized by Goward et al. (1998). The earliest known collections in the Maritimes were made in 1784 and 1785 by the Scottish surgeon–botanist Archibald Menzies while he was stationed at Halifax with the British Royal Navy. Fifteen species are represented among this material, including the type specimen of Usnea trichodea Ach., described by the Swedish lichenologist Erik Acharius in 1803 (Galloway 1995). Menzies’ Nova Scotia collections are located in Edinburgh (E) and London (BM, Länn) — herbarium acronyms from Swedish lichenologist Erik Acharius in 1803 (Galloway 1995). record of lichen collecting in the Maritimes or eastern Quebec and John Macoun in Nova Scotia and Gaspésie, Quebec. New Brunswick, Alexander Howard MacKay in Nova Scotia, collections were made during this period by James Fowler in journals spurred inventories of floras and faunas. Noteworthy establishment of natural history societies, museums, and research journals spurred inventories of floras and faunas. Noteworthy collections were made during this period by James Fowler in New Brunswick, Alexander Howard MacKay in Nova Scotia, and John Macoun in Nova Scotia and Gaspésie, Quebec.

Several American collectors were drawn to the Gaspé region, especially the Chic-Choc Mountains, in the early to mid 1900s (see Goward et al. 1998). More extensive collecting in the Bas St-Laurent region and Gaspésie was undertaken in the 1930s and 1940s by Ernest Lepage. This work formed the basis of a catalogue of Quebec lichens (Lepage 1947–1949, 1958, 1972), which included many records contributed by Frère Marie-Anselme from the Shefford region in the Appalachian foothills of southeastern Quebec. An intensive survey by Sirois et al. (1988) of ultramafic rocks and soils on the elevated, open plateau of Mount Albert (900–1150 m) in the Chic-Chocs yielded many significant discoveries. Of 188 species identified in this survey, 11 were first records for North America. Similar elevations in southeastern Quebec support mostly closed forests dominated by balsam fir (Abies balsamea (L.) Mill), not tundra or krummholz. However, the lichens of this area remain little studied (LeBlanc 1963; Clayden 2006). The largest collections of lichens from Gaspésie and other areas of eastern Quebec are located in the herbaria of l’Université Laval (QFA), with smaller numbers at the New Brunswick Museum (NBM) and Canadian Museum of Nature (CANL).

In the Maritimes, a pattern of sporadic, limited collecting continued up to the mid 1900s. Lamb (1954) produced the first critical treatment of the lichens of any part of the ecozone, reporting 199 species for Cape Breton Island on the basis of three months of field work in 1952 and revision of earlier collections made by John Macoun. Systematic studies of lichens were, in Lamb’s time, undergoing a renaissance internationally. With the more recent introduction of molecular genetic tools and characters, and increasing concern for conservation of lichens and their habitats, this research activity continues apace. Many crustose and several difficult malirolchen genera of temperate, boreal, and arctic regions have been revised in recent years, and treatments of relatively well-known European lichen bio- tasts have informed studies in North America. Thus, when Selva et al. (2004) surveyed epiphytic lichens in hardwood forests in northern Cape Breton, they recorded 175 species, 108 of which had not been reported by Lamb (1954) 50 years earlier. Comparable increases in the known diversity of other lichen-rich habitats can be expected in this ecologically diverse portion of the ecozone.

Fundy National Park, with an area of 200 km², is the only part of the AME in which the lichens of all habitats and substrates have been comprehensively surveyed. Gowan and Brodo (1988) reported 470 species for the park based on collections of c. 3500 specimens. Nearly 70% of these species were first records for New Brunswick, a telling measure of the previous state of knowledge of this province’s lichen biota. During the past few decades, many other areas of the Maritimes have been partially surveyed. Among those who have made substantial collections are F. Anderson, I.M. Brodo, R.P. Cameron, K. Casselman, S.R. Clayden, K.E. Driscoll, K. Egger, S.P. Gowan, H. Harries, H.R. Hinds, A. Koffman, W.S.G. Maass, M. Maxfield, R.T. McMullin, T. Neily, D.H.S. Richardson, D.L. Sabine, S.B. Selva, and C. Sneddon (collections at CANL, NBM, NSPM, UMFK). Other major collections have resulted from lichen forays near Liverpool and Parrsboro, Nova Scotia, in 1999 and 2004 (collections at, for example, FH, H, OMA, and NY, in addition to the above-noted herbaria). At these “Tuckerman Workshops”, about 30 experienced lichenologists met for 4 days to collect and identify lichens from a range of sites and habitats.

In addition to general inventories, studies of particular groups of species or lichen-rich community types have contributed significantly to knowledge of the regional biota (see Goward et al. (1998) for references up to 1997). For example, Selva (1994, 2003) has pursued a long-term research program aimed at assessing the diversity of calcioid lichens and fungi as indicators of the historical–ecological continuity of old-growth forests in the Acadia Forest region. Maass (e.g., 1981, 1983; Maass et al. 1986) has made detailed ecological studies, and mapped the distributions, of several rare epiphytic lichens restricted to the oceanic climatic sectors or other portions of the region. Several surveys and ecological studies of forest lichens in Nova Scotia have been published (e.g., Cameron 2002; Selva et al. 2004; Richardson and Cameron 2004; Cameron and Richardson 2006; McMullin et al. 2008). And wide-ranging taxonomic revisions of a number of genera have cited numerous collections from the AME (e.g., Brodo and Hawksworth 1977; Brodo 1984, 1991; Gowan 1989; Arup 1994; Ekman 1996; Selva and Tibell 1999). Prince Edward Island remains relatively little investigated. Although it has been greatly mod-
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ified by forest clearance for agriculture, remnants of mature forest and a range of other lichen-rich communities persist on the island (S. Selva, S. Clayden, unpublished). Further surveys of the lichens of these habitats are much needed.

**Diversity, known and expected**

About 890 species of lichen-forming fungi are known in the ecozone. Of these, 41% form foliose and fruticose macrolichens. In addition, more than 30 species of calicioid fungi in the Mycocaliciccales are present (Selva 2003; Selva and Clayden, unpublished). Lichenicolous fungi other than calicioid taxa remain very poorly documented, with fewer than 40 species recorded. These totals are based on published records and on many as yet unpublished collections located in the herbaria previously noted. A number of older collections, particularly among those cited for the Quebec portion of the ecozone by Lepage (1947–1949), are in need of critical revision.

How do these numbers compare with the diversities known in other predominantly temperate to boreal regions of North America and Europe? To assess the state of knowledge of the lichen biota of the AME, comparative data were compiled from several recent checklists and catalogues (Tables 2–4). Documented species diversity is consistently higher in northwestern European than in northeastern North American regions. Compilations of other European lichen biotas, not shown here, would reinforce this contrast. Part of the disparity can be attributed to the species–area relationship. For example, summing the areas and species diversities of the AME and New York state gives totals of 334 km² and 1160 species. Their combined area is close to that of Finland or the British Isles. But while the geological and bioclimatic diversity of these regions is roughly comparable, species diversity in Finland and the British Isles exceeds that of the combined AME and New York state by 28 and 52% (327 and 604 species), respectively. Taxonomic uncertainties account for another portion of these differences. For example, many “orphaned species” (Feuerer and Hawksworth 2007) in large, problematic genera such as *Bacidia*, *Caloplaca*, *Lecanora*, *Micarea*, *Rhizocarpon*, and *Rinodina*, 2–5 times as many species are known in northwestern Europe as in northeastern North America (Table 4). There are, however, a few notable exceptions to this generalization among genera that have been intensively investigated in the AME by specialists. For example, studies by S. Selva and colleagues have documented 18 *Chaenotheca* species in the ecozone (e.g., Selva and Tibell 1999; Tibell and Koffman 2002; Selva 2003). All but two of these also occur in Fennoscandia, which in turn has two species not yet recorded in the AME, for an identical total of 18 (Santesson et al. 2004).

Parity of species numbers is also seen in the lichenicolous and saprophytic calicioid genera *Chaenothecopsis* and *Phaeocalicium*. In these, totals of about 25 species have been recorded in each region (Selva 2003; Selva and Clayden, unpublished data; Santesson et al. 2004). These cases, as well as the relatively small differential among the recorded diversity of macrolichens (Table 3), suggest that the representation of crustose species in the ecozone, and in northeastern North America generally, is much under-recorded. An alternative explanation could be that the ratio of microlichen to macrolichen diversity is much higher in northwestern Europe than in northeastern North America, though this seems unlikely.

Macrolichens are more evenly recorded across the two continents (Tables 2, 3), as they are more conspicuous and better represented in collections. The comparatively high diversities in the AME of genera such as *Bryoria* and *Stereocaulon* are indicative of the boreal and oceanic character of the regional climate and vegetation — see below. *Usnea* is also strongly represented in the ecozone, owing to an admixture of boreal and temperate species, including several restricted to oceanic climatic sectors. Species richness in the crustose genera *Ochrolechia* and *Pertusaria* is relatively high for similar reasons. In each case, arctic–alpine, boreal, and temperate species

| Table 2. Diversity of lichen-forming and calicioid fungi known in the Atlantic Maritime Ecozone and several other regions. See Table 3 for data sources. |
|---|---|---|---|---|
| **Area (10³ km²)** | **Species diversity** | **Genera with ≥15 species** | **Genera with ≥25 species** | **Macrolichen genera with ≥10 species** |
| AME | 206 | c. 920 | 13, 8 c | 4, 2 c | 10 |
| New York | 128 | 808 | 10, 7 c | 3, 2 c | 6 |
| Michigan | 151 | 790 | 10, 6 c | 3, 2 c | 8 |
| Southern Ontario | 104 | 465 | 4, 2 c | 2, 1 c | 6 |
| British Isles | 314 | 1764 | 25, 15 c | 15, 12 c | 10 |
| Finland | 338 | 1487 | 21, 15 c | 13, 11 c | 9 |
| Fennoscandia | 1112 | 2414 | 35, 26 c | 21, 16 c | 11 |

*Total number of genera and number of crustose genera (c) among these.*
are present in the ecozone.

With further collecting and study, especially of microlichens, the diversity of lichen-forming fungi known in the AME will very likely exceed 1000 species. Scaling conservatively from a comparatively well-known area like Finland suggests that totals of 1150 species are possible. The study of lichenicolous fungi in the ecozone has scarcely begun, and it is reasonable to expect the addition of 100 or more species to the fewer than 40 recorded to date.

Despite these inferences, there are clearly genuine, sharp contrasts in the species richness of some genera between north-temperate to boreal regions of northeastern North America and northwestern Europe. *Opegrapha*, for example, is represented in the British Isles and Fennoscandia by 25 and 37 species, respectively, but by 5 or fewer recorded species in northeastern North American regions (totals in both cases including lichen-forming and lichenicolous species). The disparity in *Arthonia* species diversity (Table 4) is also unlikely to be an artefact only of differing collecting intensities. These two genera, like most Arthoniales (Table 1), have largely temperate to tropical distributions. *Opegrapha* and many *Arthonia* species are lichenized with *Trentepohlia*, though some invade the thalli of other, non-arthonialean lichens. The oceanic climate of northwestern Europe has apparently favoured their immigration, persistence, or diversification to a greater extent than has the more continental climate of northeastern North America. Species richness in these genera in coastal western North America and western Europe. Another contrast unrelated to collecting intensity is provided by *Toninia*. This genus is represented in the AME and most of eastern North America only by *T. sedifolia*, but by about 20 species in interior western North America (Timdal 1991), 16 in the British Isles (Coppins 2002), and 25 in Fennoscandia (Santesson et al. 2004). Most *Toninia* species occur on calcareous substrates in arctic–alpine and (or) arid environments, sets of conditions not found widely in eastern North America.

### Distributions in global and historical context

The geographical and bioclimatic relationships of the lichens of eastern Canada and adjoining areas of the northeastern United States have attracted considerable interest (e.g., Degelius 1940; Ahti 1964, 1983; Brodo 1968; Maass 1981, 1983; Brodo and Gowan 1983; Gowan 1983; Gowan and Brodo...
Species Diversity in the Atlantic Maritime Ecozone

Table 4. Species-rich genera of microlichens in the Atlantic Maritime Ecozone and several other regions. Numbers of species are given for all genera that are among the 10 most diverse in at least one of these regions (total no. genera = 18).  

<table>
<thead>
<tr>
<th>Region</th>
<th>AME</th>
<th>NY</th>
<th>SO</th>
<th>MI</th>
<th>BI</th>
<th>FI</th>
<th>FS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (10^3 km^2)</td>
<td>206</td>
<td>128</td>
<td>104</td>
<td>151</td>
<td>314</td>
<td>338</td>
<td>1112</td>
</tr>
</tbody>
</table>

| Lecanora        | 46  | 42 | 30 | 40 | 81 | 82 | 125 |
| Pertusaria      | 25  | 20 | 11 | 17 | 36 | 28 | 43  |
| Caloplaca       | 23  | 18 | 15 | 31 | 59 | 45 | 100 |
| Rhizocarpon     | 22  | 15 | 10 | 19 | 40 | 43 | 68  |
| Lecidea*        | 21  | 36 | 8  | 13 | 45 | 92 | 142 |
| Chaeonotheca    | 18  | 9  | 6  | 12 | 13 | 15 | 18  |
| Rinodina        | 17  | 11 | 13 | 22 | 33 | 38 | 53  |
| Micarea         | 16  | 15 | 4  | 9  | 53 | 24 | 47  |
| Arthonia        | 14  | 14 | 7  | 16 | 48 | 32 | 64  |
| Verrucaria*     | 14  | 11 | 11 | 10 | 51 | 35 | 104 |
| Buellia s.l.    | 13  | 17 | 6  | 13 | 26 | 27 | 31  |
| Bacidia         | 12  | 13 | 9  | 13 | 35 | 34 | 41  |
| Ochrolechia     | 12  | 9  | 4  | 5  | 12 | 13 | 20  |
| Porpidia        | 11  | 9  | 5  | 10 | 17 | 16 | 19  |
| Acarospora*     | 6   | 8  | 6  | 9  | 19 | 22 | 39  |
| Opegrapha       | 5   | 4  | 1  | 4  | 25 | 13 | 37  |
| Aspicilia*      | 4   | 4  | 4  | 8  | 16 | 43 | 88  |
| Polypilasistia* | 4   | 0  | 1  | 2  | 18 | 11 | 43  |
| Thelidium*      | 1   | 2  | 2  | 3  | 12 | 6  | 33  |

Total (no. of species) 234 196 121 211 478 410 666
% (+ 100) of AME 1.00 0.84 0.52 0.90 2.04 1.75 2.85

*Numbers of species in the 10 most diverse genera in each region appear in boldface type. Asterisks designate genera in which the delimitation of many species is still uncertain. In Lecidea and Verrucaria, for example, many Fennoscandian species are still known only from their type localities. These genera are excluded from the ranking of the 10 most species-rich genera, and from the species totals, but are shown for completeness.

**Abbreviations and sources as in Table 3. Recent checklists unavailable for Maine and British Columbia. Order of genera follows their species-richness in the AME.

1988; Sirois et al. 1988; Clayden 1992; Wong and Brodo 1992; Selva 1994; Sullivan 1996; Hinds and Hinds 1998, 2008). No lichens are entirely restricted to the AME. Most of those occurring here have broad ranges in eastern North America, or are discontinuously to continuously distributed around the northern hemisphere. Some occur in the higher latitudes of both hemispheres, and a few are cosmopolitan. Their patterns of distribution are, in general, similar to those of vascular plants, bryophytes, and non-lichen fungi, reflecting shared responses to climate and to earth and vegetation history. At the species level, however, the ranges of most lichens are more extensive than those of vascular plants (see below). They are also, as previously noted, more responsive to gradients of precipitation and humidity.

The ranges of lichen photobionts are less well known than those of their fungal symbionts, as identifications to species require culturing and (or) molecular studies. Because photobiont specificity for lichen fungi is less narrowly constrained phylogenetically than that of lichen fungi for photobionts, it is to be expected that the ranges of photobiont species are as broad as, or broader than, those of their fungal partners. Again, however, the selectivity of symbiont associations can be dynamic ecologically and geographically (Piercey-Normore 2006; Yahr et al. 2006). One fungal species can potentially select different photobionts in different areas of its range; if these photobionts also differ subtly in ecological requirements or tolerances, the lichen partnership might in turn shift its distribution along climatic and other gradients in different regions. On the whole, however, the bioclimatic ranges of lichens are remarkably consistent across regions and continents (Ahti 1964, 1977).

It has also been shown that the availability of compatible photobionts affects the establishment and, by extension, the frequency of certain lichens, especially those that undergo resynthesis each generation, for example, Xanthoria parietina (L.) Beltr. (Ott 1987). For the same reason, the geographical ranges of some lichens might be limited by those of compatible photobionts. There is little empirical evidence bearing on these questions.

Another striking feature of lichen distributions is the frequency of wide intra- or inter-continental gaps (disjunctions), discussed more fully in the next section. This pattern, together with the considerable breadth of most species’ ranges, is generally attributed to the antiquity and slow rates of evolutionary change of lichen fungi, and to their capacity for long-distance dispersal (Culberson 1972; Jørgensen 1983; Galloway 1996). Although the fossil record is scant, it indicates that lichen-like
Chapter 8: Lichens and Allied Fungi of the Atlantic Maritime Ecozone

symbioses have existed for upwards of 600 Ma (million years) (Yuan et al. 2005). The extant genus *Anzia* is known from fossils preserved in c. 40-Ma European amber, and probably diverged from other genera of lichen fungi before the Tertiary period (Rikkainen and Poinar 2002). Its phylogenetic position within the Lecanorales implies that many other extant genera of lichen fungi are as least as old. Estimation of the ages of genera and species of lichen fungi from molecular clocks (i.e., calibrated rates of nucleotide substitution in DNA sequences) is a recent development. In the first such study, Printzen and Lumbsch (2000) inferred that speciation within *Biatora*, a common genus in the forests of the AME, began in the late Cretaceous. The divergence times of several extant *Biatora* species were estimated to range from about 90 Ma to 10 Ma.

Long-distance dispersal of lichens or of their separate components via spores or lightweight vegetative propagules is not easily assessed directly, but soredia are often recovered in aerobiological sampling (e.g., Marshall 1996; Tormo et al. 2001). Colonization and distribution patterns provide strong indirect evidence for long-range transport of propagules by wind (e.g., Jørgensen 1983; Tibell 1994; Muñoz et al. 2004) and birds (e.g., Bailey and James 1979). Among calicioid lichens and fungi, the species with the broadest ranges are those with the smallest, most readily wind-dispersed ascospores (Tibell 1994). Phylogeographic studies based on DNA now make it possible to probe the extent and rates of gene flow among populations in a historical–evolutionary framework. One can gauge, for example, whether widely disjunct populations of species are fragments of formerly continuous ranges, among which gene flow is presently limited or lacking, or if such populations have arisen and remain interconnected by ongoing long-range dispersal of propagules or gametes.

Two contrasting examples of species occurring in the AME illustrate the potential of this approach: *Cavernularia huiltenii* Degel, is restricted to the most climatically oceanic sectors of the boreal zone in western and eastern North America, and northwestern Europe, where it occurs mainly on twigs of spruce and fir. In the AME, it is a rare lichen known only from a narrow band along the Atlantic coast of Nova Scotia, and a few islands in the outer Bay of Fundy (Maass 1981, and pers. comm., 2008). It is more widespread in Newfoundland, reaching its northern limit in coastal southern Labrador (Maass 1981). Printzen et al. (2003) found that the highly disjunct eastern North American, western North American, and European populations of this species share several ancestral nuclear ribosomal DNA haplotypes. However, each population is clearly differentiated by derived haplotypes not occurring in the other portions of the overall range. This pattern is best explained by disruption of an older, more coherent range. On geological and paleoclimatic evidence, Printzen et al. (2003) inferred that *C. huiltenii* formerly occurred more continuously at a high latitude, probably around the Arctic Ocean. Onset of the Pleistocene glaciations 2–3 Ma may have initiated or hastened the southward displacement and fragmentation of its range.

A quite different phylogeographic history has been demonstrated for *Porpidia flavicunda* (Ach.) Gowan (Buschbom 2007). In the AME, this circumpolar, arctic–alpine, rock-encrusting species is known only from higher elevations in Gaspésie and northern New Brunswick. It probably occurred more widely here during and following deglaciation, but became confined to cold, montane locations as bioclimatic zones shifted northward and upward during the Holocene. Sampling of populations of *P. flavicunda* from subarctic Quebec (Schefferville, 55°N), Baffin Island, Greenland, and northern Scandinavia has shown (i) that the geographic and genetic distances separating these populations are positively correlated, but (ii) that recurrent gene flow via long-distance dispersal of propagules has been sufficient to prevent strong population differentiation (Buschbom 2007).

These patterns of geographic structuring of genetic diversity within individual species are consistent with the overall gradient of increasing latitudinal differentiation of lichen biotas from north to south around the northern hemisphere (see Ahti 1964, 1977). At higher latitudes, the potential for reproductive isolation and speciation of populations has evidently been more constrained, owing to their shared Pleistocene glacial histories, the greater homogeneity of ecological conditions, and relative proximity of major land masses — the latter increasing the likelihood of transfer of propagules across oceans. Species occurring in boreal to arctic bioclimates are consequently more likely to have ranges extending around the northern hemisphere than are temperate or tropical species. This trend can be seen clearly in the biota of the AME: in Fundy National Park, for example, 60% of the lichens with boreal affinities have circumboreal ranges, whereas only 8% of the temperate species are circumtemperate (Gowan and Brodo 1988). On the subalpine to alpine plateau of Mount Albert, 98% (117 of 119) of the species with ranges attaining or centred in arctic latitudes are circumpolar (Sirois et al. 1988).

Until recently, it was widely held that extensive, emergent areas of the now-submerged continental shelf adjoining Atlantic Canada remained ice-free during the last glacial maximum. Along with interior nunataks and coastal cliffs, these areas were inferred to have been refugia for hardy biota able to recolonize neighbouring areas following deglaciation (Pielou 1991). Improved dating techniques and modelling of ice streams (Dyke et al. 2002; Shaw et al. 2006; ACID Workgroup 2007) do not support this interpretation. It is now recognized that late Wisconsinan glaciers covered the entire region, crossing the continental shelf to its outer edge, and capping the highest interior elevations. Only a narrow crescent of emergent shelf on the periphery of the Grand Banks, c. 500–700 km seaward of the easternmost extent of the AME in Cape Breton, might have remained unglaciated and vegetated (Shaw et al. 2006). However, relevant fossil evidence has yet to be recovered from this area (D.J.W. Piper, pers. comm., 2005).

In this light, the current distributions of species in the AME must be understood without invoking the survival of refugial populations within or adjoining the ecozone during full glacial conditions. A similar point has been made by Ahti (1983, p. 321)
in relation to the lichens of Newfoundland: these “must exhibit distribution patterns which took their shape during post-glacial migrations, and especially after the postglacial climatic optimum some 6,000 years ago”. Ahti further emphasizes the “primary importance of the present climatic conditions in deciding the existing boundaries of the ranges of both higher plants and lichens in this area”. It is of interest to examine whether this assessment holds for the lichens of the AME.

Late-glacial and Holocene eustatic and isostatic changes in relative sea level around the ecozone brought about dramatic fluctuations in coastlines and in the extent of emergence of the continental shelf (Shaw et al. 2002, 2006). These changes left what appears to be a persistent imprint on the regional flora and fauna. Most often noted is the disjunct occurrence in southern Nova Scotia of numerous Atlantic coastal plain vascular plants (Roland and Smith 1969). To these can be added several bryophytes, including, for example, Isotepgyrium tenerum (Sw.) Mitt. and Sphagnum cyclophyllum Sull. & Lesq. These plants are generally assumed to have reached Nova Scotia via early postglacial migration along the corridor of emergent shelf that extended across the outer Gulf of Maine, east and northeast from the Cape Cod area. If this scenario is correct, dispersal must also have occurred across the c. 50-km-wide Northeast Channel separating George’s Bank from Brown’s Bank (Clayden 2000).

Most of the coastal plain disjuncts in Nova Scotia occur in open wet habitats not conducive to lichens. It has been suggested, however, that many as yet undocumented coastal plain lichens probably occur in that province (Brodo and Gowan 1983). But surveys to date have revealed no disjunctions for which explanations involving migration over the formerly emergent continental shelf might be required. Several temperate eastern North American lichens are indeed known in the AME only in southern Nova Scotia (see below). But nearly all of these are found in the eastern United States as far north as central Maine. Their disjunct occurrences in Nova Scotia can be accounted for by dispersal across the Gulf of Maine to areas meeting their climatic and other ecological requirements (Clayden et al. 2010).

Other artefacts of dispersal limitations can be seen in the distributions of vascular plants in the AME that apparently lack counterparts in the lichen biota. For example, five temperate hardwood trees (Acer saccharinum L., Juglans cinerea L., Quercus macrocarpa Michx., Salix nigra Marsh., Tilia americana L.) and at least 50 herbaceous species reach the northeastern limits of their North American ranges in New Brunswick, especially in the Saint John River system (Clayden 2000). If climatic conditions were the only or the major factor limiting their ranges, many of these species would be expected to occur in Nova Scotia. Instead, a lack of suitable habitats in the extensive lowland region of southeastern New Brunswick has apparently posed an ecological barrier to their dispersal further eastward. There is no evidence of comparable differentiation between the lichen biotas of New Brunswick and Nova Scotia that might be attributable to such a barrier effect. This indicates, again, that the ranges of lichens within the ecozone are more nearly in a state of equilibrium with prevailing climatic conditions than are those of vascular plants. By extension, intensive study and mapping of lichen ranges should improve understanding of climatic variation across the ecozone.

**Disjunctions**

Disjunctions can be discerned at all geographical scales. They may arise locally because of the patchy distributions of substrates, habitats, or climatic conditions conducive to establishment, growth, and reproduction. At larger scales, the odds of dispersal between ecologically suitable, but widely separated, areas of potential occurrence are reduced, though, as noted, these odds may be affected by major wind streams or bird-migration routes. Widely disjunct populations are thus more likely, though not certain, to have longer histories of isolation, as seen in Cavernularia hultenii. The historical–migrational scenario inferred for that species by Printzen et al. (2003) is similar to one proposed by Sheard (1995) to account for the disjunct distributions of several sorediate Rinodina species. Of these, *R. degeliana* Coppins, *R. efflorescens* Malme, and *R. willeyi* Sheard & Giralt are present in the AME. In contrast to *C. hultenii*, these species are primarily epiphytes of hardwood trees in north-temperate deciduous or mixed forests. Sheard (1995) postulated that their displacement from high-latitude ranges near the Arctic Ocean began in the mid-Tertiary period.

Speciation through geographic isolation can be inferred in the case of Cladonia terrae-novae Ahti (Ahti 1961, 1977). This oceanic, temperate to boreal lichen is endemic to eastern North America, ranging from New Jersey to southern Labrador. In the AME, it is the most abundant caribou lichen (*Cladonia subgenus Cladina*) in coastal bogs, occurring also in rocky or sandy heathlands near the coast. Its fungal partner is closely related to, and perhaps nested phylogenetically within, *C. portentosa* (Dufour) Coem. s.l., which occupies similar habitats in western North America and western Europe. The widely separated populations of these species are apparently vicariants derived from a more continuously distributed common ancestor. *Cladonia boryi* is also endemic to coastal eastern North America, with geographic and ecological ranges resembling those of *C. terrae-novae*. However, it is more differentiated morphologically from its closest known relatives (e.g., *C. zopfii* Vain. of western Europe — see Stenroos et al. 2002) than are *C. terrae-novae* and *C. portentosa*.

Other lichens in the AME with disjunct, more or less oceanic, partly to largely boreal ranges include, for example, Bryoria trichodes ssp. americana (Motyka) Brodo & D. Hawksw. (recognized at species rank by most European lichen systematists), *B. bicolor* (Ehrh.) Brodo & D. Hawksw., *B. glabra* (Motyka) Brodo & D. Hawksw., *B. tenuis* (Â.E. Dahl) Brodo & D. Hawksw., *Cladonia maxima* (Asahina) Ahti, *C. metacorallifera* (Asahina), *C. norvegica* Tønsberg & Holien, *Eriderma pedicellatum* (Hue) P.M. Jörg., *Fuscopannaria ahnleri*
(P.M. Jørg.) P.M. Jørg., Hypogymnia vittata (Ach.) Parriqu, Lecidea roseoatincta Copps & Tønsberg, Mycoblastus caesius (Coppins & P. James) Tønsberg, Peligera collina (Ach.) Röhl., and Platismatia norvegica (Lynege) W.L. Culb. & C.F. Culb. (see Ahti 1977 and Holien and Tønsberg 1996). These species also occur in Newfoundland, where they are generally more frequent than in the AME. Several are found additionally at high elevations in the Appalachian mountains and other moist, high-montane areas at temperate latitudes.

A number of species occurring in the ecozone fit the well-known pattern of disjunction between eastern North America and east Asia. These are mainly inhabitants of temperate, mesic, broadleaved-deciduous, or mixed forests. No two have fully congruent ranges. All are inferred to have occurred more continuously, and at higher latitudes, across North America and Eurasia during the Tertiary period. Concrete evidence of the disruption of this continuity can be seen, for example, in the strictly fossil occurrence of Anzia in Europe, noted above. This material is referable to a section of the genus presently occurring only in east Asia and eastern North America (Rikkikinen and Poinar 2002). The American endemic A. colpodes (Ach.) Stizenb., reaches its northeastern range limit in old-growth rich hardwood and mixed forests in the AME. It is very similar to the east Asian A. colpoda Vain.

Among the species in the AME with temperate ranges disjunct between east Asia and eastern North America are Anaptychia palmulata (Michx.) Vain., Bacidia schweinitzii (Fr. ex E. Michener) A. Schneider, Cetrella cichiae (W. Culb.) W. Culb. & C. Culb., Lobaria quercizans, Myelochoroa galbina (Ach.) Elix & Hale, Ochrolechia trochorphora (Vain.) Oshio, and Parmelia fertilis Müll. Arg. Outside east Asia, P. fertilis is known only in the AME and adjoining state of Maine. Extensions of this pattern of disjunction are shown by species such as Myelochoroa aurulenta (Tuck.) Elix & Hale and Punctelia rudecsta (Ach.) Krog. In these, the eastern North American ranges extend southward into montane Central and South America; the east Asian ranges extend as far south as eastern Australia or New Zealand; and outliers are present in montane east Africa. Neither of these lichens occurs in Europe, though both are among the most common species of temperate deciduous forests in eastern North America.

Apart from oceanic and maritime (halophilic) species, disjunctions between eastern and western North America, or between both of these regions and east Asia, as seen in vascular plant genera such as Tiarella and Trillium, are apparently rare among lichens. One example, however, may be Ahtiana. All three species currently recognized in this genus are restricted to North America. Two occur in the western mountains, while A. aurescens exemplifies the so-called Appalachian – Great Lakes pattern of distribution (Brodo et al. 2001), common among the lichens of the AME. The overall range of Ahtiana suggests a phylogeographic history similar to that of other genera or species that must have had higher-latitude, more continuous distributions during the Tertiary period.

A number of lichens with temperate- to subtropical-montane ranges are disjunct between the southern and northern Appalachians and (or) coastal forests of the AME, but do not reach the boreal zone. Among these are, for example, Everniastrum catastiensi (Degel.) Hale ex Sipman, Heterodermia squamulosa (Degel.) W.L. Culb., Hypotrachyna afrorevoluta (Krog & Swinscow) Krog & Swinscow, and H. revoluta (Flörke) Hale. Pseudevernia cladonia (Tuck.) Hale & W.L. Culb. is endemic to high-elevation coniferous forests in the Appalachians and Caribbean region, and coastal or near-coastal, fog-influenced spruce–fir forests in the AME and Maine (Clayden 2006). It is possible that its montane and coastal populations had separate Pleistocene refugia. However, more recent long-distance dispersal from montane populations seems equally likely to account for the presently scattered occurrences of P. cladonia along or near the Fundy and Atlantic coasts of the AME.

An inverse pattern of distribution is evident in the endemic eastern North American Hypogymnia krogiæ Ohlsson. One of the more frequent lichens of coniferous forests in much of the ecozone, this species has outliers in montane spruce–fir stands in the southern Appalachians. It probably became isolated there after postglacial warming shifted vegetation zones and species ranges northward. A similar scenario may account for the divergence of Alectoria fallacina Motyka from A. sarmentosa (Ach.) Ach. The former is endemic to Appalachian and coastal Maritime spruce–fir forests. It is apparently derived from the wide-ranging boreal-oceanic A. sarmentosa, which must have been displaced southward during the Pleistocene (Brodo and Hawksworth 1977). The phylogeographic relationships of A. sarmentosa and A. fallacina may thus parallel those of the widespread, boreal, balsam fir, and the derived, endemic, Appalachian-montane Fraser fir (A. fraseri (Pursh) Poir.).

Bioclimatic context

Irregular topography, a deeply indented coastline, and contrasting tidal and current regimes on its Fundy, Gulf of St. Lawrence, and Atlantic shores contribute to complex bioclimatic variation in the AME. Temperature, moisture, and vegetation gradients in the ecozone are not simply orientated along continuous south–north, west–east, or coastal–inland axes. The configuration of ecoregions, within which climate and major vegetation types are fairly uniform, is accordingly in the nature of a patchwork (see Loucks 1962). Many lichens are widely distributed across this uneven background. These species have broad ecological amplitudes, or the entire ecozone is well within their overall geographical ranges. In many other cases, species have much more defined distributions within the AME. Few of these ranges are known in detail, owing to the still-modest state of survey efforts. But inferences can be made, nonetheless, about the relationship of distribution patterns to climatic variation across the ecozone. A synopsis of that variation and associated vegetation gradients is therefore presented here.

The latitudinal range of the AME is about 5.7°, from 43.5° in southern Nova Scotia to 49.2° in Gaspésie. The climate and
vegetation at low to intermediate elevations over this range fall largely within the hemiboreal zone, transitional between temperate and boreal zones to the south and north. Like other latitudinal bioclimatic zones, the hemiboreal can be traced around the northern hemisphere (Ahti 1977; Hämet-Ahti 1981; Tuhkanen 1984). In eastern North America, these zones are displaced 10° or more southward of their corresponding positions in western North America and western Europe. This shift results from the prevalence of continental over maritime air flows in the east, as well as the cooling influence of the Labrador current (Hare and Thomas 1974).

Bioclimatic variation and species ranges within the AME, as well as the comparative position of the ecozone, can be usefully summarized with reference to the circumboreal system of Tuhkanen (1984; see also Ahti 1980; Goward and Ahti 1992). This recognizes three major gradients of climate and associated vegetation: (1) a primary north–south (or comparable elevational) gradient in the amount of heat absorbed at the earth’s surface; (2) a gradient of continentality reflecting the influence of proximity to, or distance from, the ocean on the seasonal distribution of heat and moisture; and (3) a gradient of humidity. From many possible indices, Tuhkanen (1984) proposed three that can be used to situate any given area within these gradients (see Table 5). (1) Holdridge’s biotemperature is a simple measure of annual heat accumulation equal to the sum of positive monthly mean temperatures, divided by 12. In the AME, it is strongly correlated with the mean annual number of degree-days above 5°C. (2) Continentality is represented by the Conrad index. This equals the difference between the mean temperatures of the warmest and coldest months of the year, with a correction for latitude. In the Tuhkanen system, the overall (circumboreal) gradient of continentality–oceanity is divided into seven sectors (C3, C2, C1, OC, O1, O2, and O3, ranging from extremely continental (C3) to extremely oceanic (O3). Of these sectors, only two (OC, O1) are represented in the AME. (3) Humidity is approximated by the amount of precipitation received during the summer (May–August) growing season. Boundary values for these indices are given in Table 5.

The warmest and coldest portions of the ecozone are the interior of southwestern Nova Scotia, and the plateau of the Chic-Choc Mountains in Gaspésie. Mean annual temperatures in these areas are about 7–7.5°C, and −4.5°C, respectively (Environment Canada 2002; Gray and Brown 1979). The corresponding biotemperatures are about 8.0–8.3 and 3.2, with mean degree-day totals as high as 1950 and <550. These values situate southern Nova Scotia well within the north-temperate zone, and the summits of the Chic-Chocs (1000–1280 m) in the oro-hemiarctic, the elevational counterpart of the hemiarctic (Goward and Ahti 1992). Permafrost is present at these elevations (Gray and Brown 1979), and the vegetation is a shrub tundra with patches of fir and spruce krummholz. The highest elevations in the Appalachian region of southeastern Quebec (e.g., Mount Mégantic, 1105 m; Mount Gosford, 1189 m) and northern New Brunswick (Mount Carleton, 820 m) have biotemperatures of about 5.0, corresponding to middle oroboreal bioclimates. (These values are estimated here on the basis of data from the nearest climate stations, and a lapse rate of 0.6°C per 100 m of elevation.) The latter summits are well below the elevational tree limit for their latitudes (Cogbill and White 1991).

Three areas of the Maritimes have biotemperatures above 7.5 (degree-days >1730), and are referable to the north-temperate zone. A thermally equivalent area is present in southeastern Quebec in the portion of the ecozone adjoining the St. Lawrence Lowlands (Fig. 2). The 1750 degree-day isotherm shown in Fig. 2 approximates the outlines of these areas in the Maritimes: the large river valley systems of southern interior New Brunswick; southwestern interior Nova Scotia; and an area adjoining the southern and eastern sections of the Northumberland Strait. (The latter area, delimited according to a degree-day threshold of 1730, is more extensive than shown in Fig. 2.) A wide range of forest types occurs in these areas, depending on soil texture and richness, moisture conditions,
wind, fire history, and other variables (Loucks 1962). Also, as noted previously, several temperate hardwoods reach their northeastern range limits in New Brunswick, owing to their postglacial migrational histories and dispersal limitations. These species, including basswood and butternut, also occur in southeastern Quebec.

On the basis of potential evapotranspiration values above 570 mm (22.44 in.), Loucks (1962) noted that the interior of southwestern Nova Scotia can be assigned to the mesothermal category in the climatic classification system of Thornthwaite (1948). It is apparently the only such area in the Maritimes, which otherwise have cooler, microthermal climates. No tree species in the AME are confined to southern Nova Scotia. However, the forests of that area are notable for their abundant white pine (*Pinus strobus* L.), hemlock (*Tsuga canadensis* (L.) Carrière), red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.) (Loucks 1962; McMullin et al. 2008). In Maine, the isoline delineating mesothermal and microthermal areas passes through the southern part of the state, crossing the coast near Mount Desert Island (Thornthwaite 1948). Differ-entiation of the Maine lichen biota into predominantly boreal and predominantly temperate assemblages follows a similar line (Hinds and Hinds 1998). East of the St. Lawrence River in southeastern Quebec, there is also a transition from mesothermal to microthermal conditions. This follows the contact between the St. Lawrence Lowlands and the Appalachian foothills, and more or less defines the western boundary of the AME. Temperate trees such as blue-beech (*Carpinus caroliniana* Walter), shagbark hickory (*Carya ovata* (Mill.) K. Koch), and pitch pine (*Pinus rigida* Mill.) reach their limits along this boundary, as they do, further to the east, on the central coast of Maine. Except for dispersal and edaphic limitations, these species might also occur in southern Nova Scotia.

The transition between hemiboreal and boreal zones at a biotemperature of about 6.25 (Tuhkanen 1984) corresponds to a degree-day boundary value of about 1390 (Table 5). The main areas of boreal (oroboreal) bioclimates in the ecozone are at higher elevations in Gaspésie, north-central and northwestern New Brunswick, and Cape Breton Island (Fig. 2). Elevation-related ecotones between hemiboreal and boreal forests are present in each of these areas. These are definable by the upper limits of trees such as beech (*Fagus grandifiolia* Ehrh.) and sugar maple (*Acer saccharum* L.), and a corresponding shift to dominance by balsam fir and (or) black spruce (*Picea mariana* P. (Mill.) Britton, Sterns & Poggenb.), and sometimes also white spruce (*P. glauca* (Moench) Voss).
Yellow birch (*Betula alleghaniensis* Britton) and red spruce (*P. rubens* Sarg.) also reach their upper limits within the hemiboreal–boreal ecotone, though at somewhat higher elevations than beech and sugar maple. The northern range limit of red spruce crosses the northern part of the ecozone. It is correlated with a mean annual temperature of 2°C, a January mean of −13°C, and extreme minima of −40°C (Cogbill and White 1991). Red spruce is thus excluded from most of northwestern New Brunswick and Gaspésie, though it is otherwise an abundant and characteristic tree in most (not all) of the ecozone. At the highest elevations in southeastern Quebec, it is also near its climatic limit. From here northward to the Chic-Chocs, the elevation of the hemiboreal to boreal ecotone decreases by about 600 m (Cogbill and White 1991).

Near the cool Fundy and Atlantic coasts, there are also steep climatic gradients along which hemlock, white pine, sugar maple, and most other temperate trees are excluded. Red spruce and yellow birch are common in the spruce–fir forests along the Bay of Fundy, but rare or lacking in the Atlantic coastal forests of Nova Scotia, where fir and black or white spruce are dominant. These inland–coastal changes resemble, but are not identical to, the elevational ecotones in upland areas of the AME between deciduous or mixed hemiboreal forests and evergreen boreal forests. Biotemperature values for the coolest parts of the Atlantic and Fundy coasts are in the range of 6.5–6.6, suggesting that their spruce–fir communities can be considered as oceanic variants of hemiboreal forests. However, degree-day totals in these areas are 1380–1400 (Environment Canada 2002), encompassing the estimated boundary value for the hemiboreal-to-boreal ecotone (1390 degree-days, Table 5). Boreal, oceanic lichens are frequent on these coasts (see below). The forest and heathland communities along the Atlantic shore of eastern Nova Scotia in particular are similar in a number of respects to those of southern Newfoundland.

Oceanic influences are also clearly evident in the variable elevation of the hemiboreal–boreal ecotone in upland areas. The upper limit of hemiboreal forests decreases by about 400 m from west to east across the ecozone: from 760–820 m in southeastern Quebec (Gauvin and Bouchard 1983) to about 350–400 m in Cape Breton (Greenidge 1961; Gullison and Bourque 2001). Above about 450 m, the climate and vegetation of the Cape Breton plateau have strong similarities to those of the Avalon Peninsula of southeastern Newfoundland (Danman 1983). This coastward compression of elevational bioclimatic zones implies increasing temperature lapse rates. Crawford (2000) noted that rates of 0.8–1.0°C per 100 m of elevation are characteristic of oceanic regions.

On the continentality gradient, most of the Maritimes are situated in the intermediate OC sector of Tuhkanen, with Conrad index values between 35 and 50. The most continental areas, with mean January and July temperatures differing by more than 30°C, and index values of 45–50, are in western and northwestern New Brunswick, and throughout the Appalachian region of Quebec. Moderation of winter temperatures and continentality values from northwest to southeast corresponds with decreasing elevation and increasing proximity to the Fundy and Atlantic coasts. Sea surface temperatures along these coasts remain above freezing throughout the winter, but cold (7–15°C) in summer (Bousfield and Thomas 1975; Gates 1975), owing to strong tidal mixing in the Bay of Fundy and the influence of the Labrador current. In contrast, the southern Gulf of St. Lawrence and Northumberland Strait are ice-covered in winter, but thermally well stratified in summer, with mean July–August surface temperatures 17–20°C. As a result, there is much less bioclimatic differentiation along the coastal–inland axis here than along the Fundy and Atlantic coasts. Conrad index values are 28–35 near the latter coasts, in the range of the more oceanic O1 sector in the Tuhkanen system, but 40–45 (OC sector) near the Northumberland Strait. The Îles de la Madeleine are a special case. Values for biotemperature (6.2), degree-days (1323), and the Conrad index (36) situate these islands in the transition between hemiboreal and southern boreal zones, and between OC and O1 continentality sectors.

Although the Conrad index represents the thermal component of continentality, it is also correlated with the seasonal distribution of precipitation. Summer (May–August) rainfall in the more continental areas of the ecozone accounts for about 40% of annual precipitation totals. In the more oceanic O1 sector, precipitation is more equably distributed, with the summer:annual ratio ranging from 25 to 30%. Near the Fundy and Atlantic coasts, 85% or more of precipitation falls as rain. Inland, this proportion decreases to 70–75% over most of the ecozone. At high elevations in Gaspésie, about half of all precipitation is in the form of snow. Most of the ecozone has summer rainfall totals above 300 mm (range c. 320–500 mm), and is therefore in the wettest, “perhumid” category on the humidity gradient of Tuhkanen (1984). The lowlands of eastern New Brunswick and north-central Nova Scotia, Prince Edward Island, and the Annapolis Valley have lower summer rainfall amounts than other comparably warm areas, and are humid, rather than perhumid. Rainfall amounts are higher on the windward aspects of hill ranges, and rain shadows form on leeward slopes, plains, and valleys (Loucks 1962; Clayden 2000). The Îles de la Madeleine have the lowest May–August rainfall in the ecozone (263 mm; 1961–1990 normals). However, the summer:annual precipitation ratio (27%) on these islands is similar to that of Fundy and Atlantic coastal areas.

Thornthwaite’s (1948) moisture index is a more complex measure of humidity and aridity. It provides a somewhat finer, though complementary, subdivision of the humidity gradient (Fig. 3) that is also helpful in interpreting lichen distribution patterns in the ecozone. Four of Thornthwaite’s humidity categories are represented in the AME: perhumid (A) and three humid subcategories (B4, B3, B2). The entire Atlantic slope of Nova Scotia, the Fundy coast of New Brunswick, and the highlands of Cape Breton are perhumid in this system. Next in order of humidity are the areas inland of the perhumid coasts, along with the highlands of north-central and northwestern New Brunswick, Gaspésie, and southeastern Quebec. Intermediate conditions are found in north-central Nova Scotia, the
Annapolis Valley, and at low to moderate elevations over most of New Brunswick and Gaspésie. Humidity is lowest (B2 sub-category) in portions of western and northwestern New Brunswick, the Bas St-Laurent region of Quebec, and in the rain shadow of the Chic-Chocs on the northern and eastern coastal areas of Gaspésie (Fig. 3).

The Fundy and Atlantic coasts, along with those of southern Newfoundland, are among the foggiest in the world (Hare and Thomas 1974). Marine advection fog occurs on average about 2000 h per year (23% of all hours) in some coastal areas of southern Nova Scotia (Beauchamp et al. 1998). At Letete on the north shore of the Bay of Fundy, average fog duration from April to October, the period of highest frequency, is 880 h (Cox et al. 1989). There are 90–120 days per year on which these coasts are fogbound for an hour or more, versus 30–60 days in the Gulf of St. Lawrence and Northumberland Strait (Gates 1975; Muraca et al. 2001). Fog reduces estimated annual evapotranspiration in the Fundy and Atlantic coastal belts by up to 6%; liquid water inputs to the landscape are increased by up to 8% and stream flow volumes by about 10% (Yin and Arp 1994). Fog, as cloud, is also a significant influence in montane areas of the ecozone (Schemenauer et al. 1995). In the northern Appalachians, higher elevations are immersed in cloud for 30–50% of all hours (Mohnen 1992). Clouds contain more liquid water than low-elevation fog, and their inputs to the water budgets of montane forests are thus more substantial (Yin and Arp 1994). Even relatively low-elevation hills (300–500 m) in the AME are often within the cloud base on overcast days (Loucks 1962).

The number of days with measurable rainfall is another useful gauge of the humidity available to lichens (Coppins 1976; Holien and Tønsberg 1996). This parameter is defined in Canadian climate normals as days with ≥0.2 mm of rain. On this basis, the number of rainy days per year in the AME ranges from 88 to 157. (In comparison, the oceanic climates of northwestern Europe have more rainy days, but comparable rainfall totals.) Rainfall frequency in the AME is inversely correlated with the continentality index, though there are local departures from this trend. The number of rainy days is highest along the Fundy and Atlantic coasts. It is lowest in parts of central, northern, and northwestern New Brunswick, as well as in the Bas St-Laurent, Gaspé, and Îles de la Madeleine regions of Quebec.

Fig. 3. Humidity sectors in the Atlantic Maritime Ecozone, delimited according to Thornthwaite’s moisture index, 1941–1970 normals; more humid sectors have higher index values. Adapted from Phillips et al. (1990), and reproduced with the permission of Natural Resources Canada 2008, courtesy of the National Atlas of Canada.
Species Diversity in the Atlantic Maritime Ecozone

Table 6. Bioclimatic spectrum of lichen biotas in two areas of the Atlantic Maritime Ecozone, and in the adjoining state of Maine. The numbers in each bioclimatic zone (arctic, boreal, temperate, subtropical) are the proportions of species with distributions centred in that zone, including subzones.

<table>
<thead>
<tr>
<th>Species group</th>
<th>Mt Albert plateau, Quebec</th>
<th>Fundy National Park, New Brunswick</th>
<th>Maine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species diversity</td>
<td>All lichens</td>
<td>All lichens</td>
<td>Macrolichens</td>
</tr>
<tr>
<td>Elevation range (m)</td>
<td>900–1150</td>
<td>0–380</td>
<td>0–1600</td>
</tr>
<tr>
<td>Arctic</td>
<td>0.47</td>
<td>0.06</td>
<td>0.18</td>
</tr>
<tr>
<td>Boreal</td>
<td>0.38</td>
<td>0.33</td>
<td>0.40</td>
</tr>
<tr>
<td>Temperate</td>
<td>0.14</td>
<td>0.56</td>
<td>0.34</td>
</tr>
<tr>
<td>Subtropical</td>
<td>0.00</td>
<td>0.05</td>
<td>0.08</td>
</tr>
</tbody>
</table>

*Siros et al. 1988.
*Gowan and Brodo 1988.

Distribution patterns in the ecozone

Table 6 shows the zonal bioclimatic profiles (arctic to subtropical) of the lichens in two contrasting portions of the AME, and of the macrolichens in the adjoining state of Maine. These summaries illustrate the considerable regional differentiation of the biota in the ecozone. In the following section, generalized patterns of distribution of lichens within the AME are outlined and interpreted in the bioclimatic framework presented above. The individualism of species makes the delineation and interpretation of such patterns difficult. This effort is complicated by the spottiness of occurrence data available for most species. The result is a preliminary and tentative classification open to revision and improvement through future field, herbarium, cartographic, and other studies.

1. Chic-Chocs, orohemiarctic

These species occur on rock, soil, and humus, or over bryophytes, dwarf vascular plants, and plant debris on the orohemiarctic summits of the Chic-Chocs. Some, like Caloplaca tetraspora (Nyl.) H. Olivier, Lecanora epibryon (Ach.) Ach., Polyblastia cupularis A. Massal., P. hyperborea Th. Fr., Rinodina calcigena (Th. Fr.) Lynge, and Vidpicida tilesii (Ach.) J.-E. Mattsson & M.J. Lai, are found on calcareous substrates. Most are acidophiles. A partial list of these includes Alectoria ochroleuca (Hoffm.) A. Massal., Bellemerea cinereoargentea (Ach.) Clauss & Cl. Roux, Belonia russia (Körb. ex Nyl., Bryocaulon divergens (Ach.) Kärnefelt, Buellia papillata (Sommerf.) Tuck., Catillaria muscicola Lynge, Catolechia whalenbergii (Ach.) Flot., Cladonia bellidiflora (Ach.) Schäfer., C. cyanipes (Sommerf.) Nyl., C. macroceras (Delise) Ahti, C. trassii Ahti, Lecidella wulfenii (Ach.) Köhr., Lecidosa demissum (Rutstr.) Goth. Schneid. & Hertel, Ochrolechia gyalactea (Nyl.) Zahlbr., O. inaequataula (Nyl.) Zahlbr., O. upsaliensis (L.) A. Massal., Pertusaria coriacea (Th. Fr.) Th. Fr., P. dactylina (Ach.) Nyl., P. octomela (Norman) Erichsen, P. panryga (Ach.) A. Massal., Rhizocarpon rittkense (Hellb.) Th. Fr., R. superficiale (Schäfer) Malme, Sporastatia testudinea (Ach.) A. Massal., Stereocaulon alpinum Laurer, S. botryosum Ach., S. symphychellum I.M. Lamb, Thamnolia vernicularis var. subuliformis (Ehrh.) Schäfer., and Tremolecia atrata (Ach.) Hertel. Several of these species occur at much lower elevations on the oceanic (O1), southern boreal, Avalon Peninsula of eastern Newfoundland. It is likely that some of them will be found in the highlands of Cape Breton and northern New Brunswick.

Scattered late snowbeds are present in the Chic-Chocs, especially on Mount Jacques-Cartier. These are inhabited by a number of rare, phytogeographically interesting bryophytes (Belland and Favreau 1988). However, the lichen assemblages in these sites have as yet received no special attention. Cladonia ecnocyna Leight. and C. trassii occur mainly in these habitats, and another snowbed species, Solorina crocea (L.) Ach., has been reported (Dodge 1926), though not confirmed from the Chic-Chocs. The high-elevation lichen biota of this area is known mainly through the survey by Siros et al. (1988) of the geologically unusual plateau of Mount Albert. This consists of serpentinized peridotite, with a border of amphibolite. As on similar ultramafic rocks in western Newfoundland (Ahti 1983), no specialized serpentinicolous lichens are present. Lichen cover on the serpentine is <3% but >30% on the adjoining amphibolite, which has much lower concentrations of magnesium, nickel, and chromium (Siros et al. 1988). With further exploration, numerous additions to the lichen biota of the Chic-Chocs can be expected.

2. High elevation, Chic-Chocs and other areas, oroboreal to orohemiarctic

Apart from Mount Albert, high elevations in the ecozone have been surveyed only thinly and cursorily for lichens. Talus slopes, bluffs, and rocky heaths in these areas have a high diversity of saxicolous crustose species, but these remain little collected. A few conspicuous crusts and macrolichens are somewhat better documented and suggest distribution patterns likely to be replicated by those of other species. For example, Ophioparma ventosa (L.) Norman is known from the Chic-
Chocs, Mount Carleton, and Serpentine Mountain in northern New Brunswick, and Mount Gosford in southeastern Quebec. *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell, *F. nivalis* (L.) Kärnefelt & A. Thell and *Orphniospora moriopsis* (A. Massal.) D. Hawksw. occur in these areas (with the exception of Mount Gosford) and also in the Cape Breton Highlands. *Stereocaulon grande* (H. Magn.) H. Magn. and *S. paschale* (L.) Hoffm. are likewise found in Cape Breton, northern New Brunswick, and Gaspésie, but are not strictly montane in the latter two areas. *Rhizocarpon eutetraeoides* (Nyl.) Blomb. & Forssell and *R. radioatum* (Flörke ex Spreng.) Th. Fr. are so far known only from the Chic-Chocs and northern New Brunswick, as are the macrolichens *Cetraria ericetorum* Opiz, *C. laevigata* Rass., and *Umbilicaria torrefacta* (Lightf.) Schrad. *Alectoria nigricans* (Ach.) Nyl. is frequent in dwarf shrub and moss (*Racomitrium lanuginosum*) heaths on Mount Albert, but known elsewhere in the ecozone only from the Cape Breton plateau. The only known occurrence in the AME of *Varicellaria rhodocarpa* (Körb.) Th. Fr. is also on this plateau (Thomson 1997). Exceptionally strong winds, locally known as “suêtes”, affect the Cape Breton highlands and coastal areas on its northeastern flank. These can sweep exposed knolls and boulders more or less free of snow in winter, despite otherwise high regional snowfall amounts. Intensive examination of such sites will likely reveal the presence of other arctic species tolerant of extreme conditions, but intolerant of prolonged snow cover.

3. High elevation (northern) and cool coastal, hemiboreal to oroalpine

Species in this group have distributions resembling those in the last, but are also known from the Fundy and (or) Atlantic coastal comparables are discernible in the vascular and bryophyte floras of New Brunswick and Nova Scotia (e.g., Schofield 1955; Belland and Schofield 1994; Clayden 2000). The overall distributions of these lichens extend from the arctic or northern boreal to the north-temperate zone. In the AME, they are strictly northern (high elevation) and southern (coastal), occurring in a range of habitats. The arctic–alpine species *Bryoria nitidula* (Th. Fr.) Brodo & D. Hawksw. and *Sphaerophorus fragilis* (L.) Pers. are found disjunctly on scattered windswept rock outcrops on the Atlantic coast of Nova Scotia, where intermittent winter snow cover exposes them to low temperatures. *Cetraria aculeata* (Schreb.) Fr. has a similar overall (i.e., mainly arctic) distribution, but occurs in a wider range of coastal habitats and locations in the AME, including sand dunes in the Îles de la Madeleine and other areas adjoining the Gulf of St. Lawrence. *Arthrorhaphis citrinella* (Ach.) Poelt colonizes disturbed mineral soils, often along roadsides. Another set of uncommon to rare species occurs on cliffs or ledges in cool, moist ravines, along waterways, or on cool talus slopes, especially along the Bay of Fundy. Among these are *Amygdalaria panaeola* (Ach.) Hertel & Brodo, *Cladonia macrophylla* (Schær.) Stenh., *C. metacorallifera* Asahina, *Clauzadeana macula* (Taylor) Coppins & Rambold, *Nephroma arcticum* (L.) Torss., *Peltigera scabrosa* Th. Fr., *Pertusaria subobduces* Nyl., *Stereocaulon subcoralloides* Nyl., and *Umbilicaria vellea* (L.) Ach. s. str. *Sphaerophorus globosus* (Huds.) Vain. is found in these habitats and locations, but also on tree bases in moist spruce–fir forests. In Nova Scotia, it extends further inland in such stands than in New Brunswick; however, it is increasingly confined to old-growth forests along the coastal–inland gradient.

Atlantic and Fundy coastal bogs likewise have scattered populations of northern species, all rare in these locations. Examples are *Cetrariella delisei* (Bory ex Schae.) Kärnefelt & A. Thell, *Cladonia wainioi* Savicz (also in rocky, open heath in a Fundy coastal ravine), and *Ochrolechia frigida* (Sw.) Lyng (known also from peatlands on Miscou Island at the northeastern tip of New Brunswick). The latter two species are moderately frequent in bogs on the plateau of Cape Breton Island (Comeau and Beil 1984), and *C. wainioi* occurs in rocky heaths on higher summits in northern New Brunswick.

4. Northern and cool coastal, hemiboreal to boreal, oceanic

The ecological and geographic ranges of these species overlap those in the previous group. For example, *Alectoria sarmentosa* (Ach.) Ach., *Hypogymnia vittata* (Ach.) Parrique, and *Mycolastus affinis* (Schae.) T. Schauer, much like *Sphaerophorus globosus* (Huds.) Vain., are found on coniferous tree trunks and branches, or on mossy rocks, in ravines, and moist coastal spruce–fir forests. Unlike *S. globosus*, however, they do not extend into treeless, hemiarctic environments within the AME. But like the forest-inhabiting populations of *S. globosus*, they are increasingly restricted, with increasing distance from the coast, to moist old-growth stands. In these, long-term continuity of mature tree cover, as well as the accumulation of biomass in thick organic soil layers, snags, and rotting logs, maintains high relative humidity. Comparable moisture conditions may be created by a high water table, or near watercourses, but the presence of mature forest cover is generally also a requirement. There are also a few forest floor species in this category, including *Peltigera neopolydactyla* (Gyeln.) Gyeln.

*Bactrospora brodii* Egea & Torrente, *Bryoria bicolour* (Ehr.) Brodo & D. Hawksw., *B. friabilis* Brodo & D. Hawksw., *B. implexa* (Hoffm.) Brodo & D. Hawksw., *Myco- blotus caesius*, and *Protopannaria pezioides* (Weber ex F.H. Wigg.) P.M. Jörg. & S. Ekm are further examples of species disjunct between southern coastal and northern forests in the ecozone. *Peltigera collina* is known from the island of Grand Manan in the outer Bay of Fundy, and upland forests in Cape Breton and Gaspésie. *Platismatia norvegica* occurs in the Cape Breton Highlands, and was also found near Mount Carleton in northern New Brunswick in the late nineteenth century, probably in humid old-growth spruce–fir forest. This species is a characteristic element of moist coniferous forests on the island of Newfoundland (Ahti 1983), as is *Cavernularia hultenii*. But as previously noted, *C. hultenii* in the AME
occurs only at lower elevations along the Atlantic and outer Bay of Fundy coasts (see below).

5. Northern, boreal, mainly continental


Other species that are equally wide-ranging within the ecozone are, however, much less frequent. Most of these are inhabitants of old-growth forests, for example, *Buellia schaereri* De Not., *Catinaria atropurpurea* (Schaer.) Vèzda & Poelt, *Coenogonium luteum* (Dicks.) Kalb & Lücking, *Leptogium laceroides* B. de Lesd., *Megalaria grossa* (Pers. ex Nyl.) Ha-fellner, *Menegazzia terebrata* (Hoffm.) A. Måssel., *Pamaria rubiginosa* (Thunb.) Delise, *Pseudocyphellaria crocata* (L.) Vain., and *Ramalina thruxta* (Ach.) Nyl.

The diversity of temperate species occurring in hardwood forests decreases toward the northern and elevational limits of these stands in the ecozone. However, survey efforts to date have been too scant to enable mapping or ordering of species along these gradients. Variation in the tolerance of low winter temperatures is probably the main factor contributing to the northward or elevational decline in diversity. In a few cases, the range limits of species coincide with those of the trees on which they chiefly occur. For example, *Pyrenula pseudobufonius* (Rehm) R.C. Harris is absent from hardwood stands in the Mount Carleton area, as are beech and red oak, its main phorophytes. (Most of the temperate to hemiboreal hardwoods and conifers occurring in the AME do not reach Newfoundland, which, on climatic grounds, has little or no representation of the hemiboreal zone. Yellow birch is an exception among the hardwoods, and white and red (*Pinus resinosa*) pines, among the conifers; however, the diversity of lichens occurring on yellow birch is lower in Newfoundland than in the AME.)

Several corticolous macrolichens that are frequent in north-temperate or hemiboreal forests across much of the ecozone are curiously rare or lacking in eastern Nova Scotia and Cape Breton. Notable among these are, for example, *Usnicetaria oakesiana* (Tuck.) M.J. Lai & J.C. Wei and *Hypogymnia krogiae*. These species are approximately sympatric in eastern North America, extending southward at higher elevations in the Appalachians. But *U. oakesiana* is also found in
the Great Lakes region, whereas \textit{H. krojiae} is restricted to the somewhat cooler, wetter bioclimates of the AME, Maine, and the southern Laurentians of Quebec. (As noted above, the latter range approximates that of red spruce.) These differences suggest that the roughly coincident, eastern limits in the AME of \textit{U. oakesiana} and \textit{H. krojiae} are probably determined by differing climatic and (or) biotic factors, though the consequences for their distributions are similar.

A disproportionate number of the macrolichens showing this pattern of exclusion or near-exclusion from the easternmost part of the ecozone are fertile species lacking joint fungal–algal propagules. (\textit{Usnocetraria oakesiana} is an exception. In the AME, apotheciate thalli in this species are known only from montane coniferous forests in the Appalachians of southeastern Quebec.) Other examples among species occurring primarily on conifers are \textit{Ahitiana aurescens} (Tuck.) A. Thell & Randlane and \textit{Platismatia tuckermanii} (Oakes) W.L. Culb. & C.F. Culb., the latter rare in Cape Breton (Selva et al. 2004) and Newfoundland (Ahti 1983).

Of those found mainly on hardwoods, but likewise unknown so far in Cape Breton, \textit{Anaptychia palmulata}, \textit{Anzia colpodes} (Ach.) Stizemb., and \textit{Parmelia fertilis} may be noted. A further example is \textit{Melanohalea septentrionalis} (Lyng) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch, a very common boreal and hemiboreal species in much of the ecozone, occurring mainly on alders, and smooth branches of red maple, willows, and other shade-intolerant hardwoods with moderately acidic bark. On thermal and vegetational criteria, any of these lichens should potentially occur on Cape Breton Island. Their absence, if borne out by further field studies, might involve obstacles to their resynthesis from separately propagated fungal and algal biions. Climatic or biotic factors affecting the germination of ascospores, survival of sporelings, or availability of compatible photobionts might be proximate causes.

\section*{7. High elevation (southern) and cool coastal, hemiboreal}

Species in this group were noted above in the description of patterns of disjunction on a continental scale. Of those disjunct within the AME between high-elevation coniferous forests in the Appalachians of southeastern Quebec, and the Fundy and Atlantic coast, two are known so far: \textit{Everniastrum catawbiense} and \textit{Pseudevernia cladonia}. In New Brunswick, a large, though very localized, population of \textit{P. cladonia} is present in old-growth spruce–fir forests at 250–300 m elevation in the Nerepis Hills, about 30 km inland from the Bay of Fundy. These hills are often immersed in localized low cloud, formed by the interception of moisture-laden air masses moving in from the coast. It is noteworthy that at least one other Appalachian-montane and coastal species, \textit{Heteroderma squamulosa}, has an isolated occurrence in this area. On a very small scale, this pattern is reminiscent of the disjunct occurrence of oceanic lichens in “inland rain forests” on the windward slopes of interior mountain ranges in western North America (Goward and Spribille 2005).

\section*{8. Southern coastal, subtropical to boreal, oceanic}

This is a relatively large and heterogeneous group. Although many lichens are known in the ecozone only from areas near the Fundy and Atlantic coasts, these species have diverse ranges outside the AME. At least four subgroups can be recognized:

\subsection*{(i) Boreal oceanic species in the AME at the southern limits of their ranges}

Of these, the best known are \textit{Cavernularia hultenii}, \textit{Erioderma pedicellatum}, and \textit{Fuscopannaria ahnleri}. \textit{Thelotrema suecicum} is a further example. These lichens are more frequent and widely distributed on the island of Newfoundland than in the AME. Declines in the frequency of \textit{E. pedicellatum} in Nova Scotia over the past several decades, and the extirpation of this species at its type locality on the Fundy coast of New Brunswick, are generally attributed mainly to air pollution, acid rain and fog, and forest clear-cutting (Maass and Yetman 2002; Cameron and Neily 2008). Another possibly contributing factor deserving of investigation is the significant decline in the frequency of Atlantic coastal fog over this period (Beauchamp et al. 1998; Muraca et al. 2001). The causes of this change are not understood (Muraca et al. 2001). The seeming decline, or perhaps disappearance, of \textit{C. hultenii} in Nova Scotia in recent years (W.S.G. Maass, pers. comm., 2008) might also be related to declining fog frequency. Like \textit{E. pedicellatum}, \textit{C. hultenii} is a very drought-sensitive species (Maass 1981). In contrast to \textit{E. pedicellatum}, however, it is an acidophile, and therefore less likely to be affected by acid rain or fog. This points to a more general inference: The greater inland penetration of boreal, oceanic, drought-sensitive species in Newfoundland may partly reflect the straightforward dependence of relative humidity on air temperature. For a given amount of water vapour in the air, relative humidity rises with decreasing temperature. This relationship might account in part for the approximately V-shaped distributions in northeastern North America of species such as \textit{Alectoria sarmentosa}, \textit{Cladonia boryi}, \textit{C. maxima}, \textit{C. terreae-novae}, and \textit{Hypogymnia vittata} (see distribution maps in Brodo et al. 2001).

\subsection*{(ii) North-temperate to boreal, oceanic species, with the eastern North American portions of their ranges approximately centred in the AME}

This subgroup is exemplified by species such as \textit{Arthonia leucopellaea} (Ach.) Almq., \textit{Clistostomum leprosum} (Räisänen) Holén & Tonsberg, \textit{Degelia plumbea} (Lightf.) P.M. Jørg. & P. James, \textit{Graphis elegans} (Borrer ex Sm.) Ach., \textit{Lecanactis abietina} (Ach.) Körb., \textit{Nephroma laevigatum} Ach., \textit{Thelotrema lepadinum} (Ach.) Ach., and \textit{Usnea flammae Stir.} These occur mainly in old-growth mixed or coniferous forests within about 20 km of the coast. \textit{Degelia plumbea} and \textit{N. laevigatum} can also occur in more nutrient-rich habitats, including red maple and arborvitae (\textit{Thuja occidentalis}) swamp forests. Most of the North American population of \textit{D. plumbea} is within the ecozone.
(iii) **Subtropical-montane to temperate oceanic species, disjunct in the AME**

Among these are *Erioderma mollissimum* (Samp.) Du Rietz, *Heteroderma squamulosa*, *Hypotrachyna afrorevoluta*, *H. revoluta*, *Parmelinopsis minarum* (Vain.) Elix & Hale, *Punctelia appalachensis* (W.L. Cub.) Krog, *Sticta fuliginosa* (Dicks.) Ach., and *S. limbata* (Sm.) Ach. Some of these lichens are also found at low elevations in temperate oceanic bioclimates in western North America, Europe, and other regions. *Punctelia appalachensis* is an eastern North American hardwood forest endemic. In North America, *Erioderma mollissimum* is known only from the Great Smoky Mountains and Atlantic Canada. Here, it is extremely rare near the Funky and Atlantic coasts of New Brunswick and Nova Scotia, and on the Avalon Peninsula of Newfoundland. It is generally associated with *Cocccarpia palmicola* (Spreng.) Arv. & D.J. Galloway and *E. pedicellatum*, the only other corticolous lichens in the ecozone with *Scytonema* photobionts (Jørgensen et al. 2009).

The various species showing these broad disjunctions do not share obvious features that might have enabled them to extend their distributions far northward of their core ranges. All of them reproduce, and are dispersed, mainly via vegetative propagules. But there are many such species that, although frequent in the central and southern Appalachians, do not reach northern New England or Atlantic Canada. The northern disjuncts seem likely to be those with a requirement for humid bioclimatic conditions in combination with a tolerance of low winter temperatures.

(iv) **Subtropical to temperate species extending more continuously northward to the AME**

Examples from various habitats, are *Chrysothrix insulicola* R.C. Harris & Ladd (Harris and Ladd 2008), *Cocccarpia palmicola*, *Cladonia atlantica* A. Evans, *C. rappii* A. Evans, *Parmotrema arnoldii* (Du Rietz) Hale, *P. crinitum* (Ach.) M. Choisy, *P. perlatum* (Huds.) M. Choisy, *Phaeogramphis inusta* (Ach.) Müll. Arg., *Punctelia caseana* Lendemer & Hodkinson, *Thelotrema subtile* Tuck., and *Usnea merrillii* Motyka. Several other *Usnea* species and additional lichens with “coastal plain” or eastern temperate distributions may also belong here. In the southeastern United States, some of the lichens in this subgroup are distributed over a wide longitudinal range. Toward the northeast, the ranges of species such as *C. palmicola* or *P. crinitum* are characteristically narrowed into the coastal region. But *C. palmicola* is less strictly confined to the coast in Nova Scotia than in New Brunswick, and also extends into the interior of Newfoundland, where it is relatively frequent in the more oceanic climatic sectors. The contrasting bioclimatic and edaphic niches of this species at the southern and northern limits of its range in eastern North America invite investigation of its genetic variation over this range.

9. **Southern interior, scattered to wide-ranging, temperate to hemiboreal**

These species are not restricted to coastal regions, unlike those in the previous group, but are similar in having mainly southern distributions within the ecozone. Those that range somewhat further north do so in relatively warm, more continental (OC) climatic sectors. The following examples are known from both New Brunswick and Nova Scotia, though not from the lowland areas linking them: *Anzia colpodes*, *Arthonia caesia* (Flot.) Körb., *Buellia dialyta* (Nyl.) Tuck., *Collerella leptaleatum* Tuck., *Fuscopannaria leucosticta* (Tuck.) P.M. Jørg., *Imshaugia placorodia* (Ach.) S.L.F. Mey., *Leptogium burnediae* C.W. Dodge, *L. corticola* (Taylor) Tuck., *L. milligranum* Sierk, *Myelochroa aurulenta* (Tuck.) Elix & Hale, *Pannaria lurida* (Mont.) Nyl., and *Trypethelium virens* Tuck. (all corticolous), *Dimelaena oreina* (Ach.) Norman and *Physcia subtilis* Degel. (saxicolous), and *Cladonia incrassata* Flörke, *C. poly-carpoide* Nyl. and *C. sobolecens* Nyl. ex Vain. (terricolous). *Dimelaena oreina* as currently circumscribed might prove to include cryptic species, as it also occurs widely, though disjunctly, in arctic regions.

10. **Southern interior, Quebec, temperate**

Temperate species known in the ecozone only from southeastern Quebec are few in number, though more may be expected. These include *Heteroderma hypoleuca* (Mühl.) Trev. and *Xanthomendoza fallax* Söchting, Kärnefelt & S.Y. Kondr. The latter species occurs on planted trees along roadsides, and may be adventive in this area.

11. **Southern interior, Nova Scotia, temperate**

As already noted, the distributions of these species somewhat resemble those of the vascular plants forming a disjunct coastal plain assemblage in interior southern Nova Scotia. Historical migrational scenarios have been advanced to account for the disjunctions in the vascular flora. In the case of the lichens, however, the equivalency of the present, local climatic conditions to those in southern and central New England suffices to account for their disjunct occurrences in Nova Scotia. Among these species are *Cetraria arenaria* Kärnefelt, *Cladonia subtenuis* (Abbeyes) A. Evans, *Flavoparmelia baltimorensis* (Gyeln. & Fóriss) Hale, *Leptogium dactylinum* Tuck., *Ochrolechia yasuda* Vain., *Parmotrema reticulatum* (Taylor) M. Choisy, *Pertsoria pustulata* (Ach.) Duby, and *Tuckermanella fendleri* (Nyl.) Essl.

12. **Coastal, halophilic, temperate to arctic**

Taylor (1974) recorded 21 species in a survey of intertidal lichens from New Jersey to Newfoundland. Of these, 10 are *Verrucaria* species, and nearly all are found throughout the northeast. This survey did not include any sites in Gaspésie, northern and eastern New Brunswick, Prince Edward Island, or the Gulf shore of Nova Scotia, and there is almost no data available on the littoral lichens of these areas.
Rocks in the supralittoral or splash zone along maritime shores of the AME also have a distinctive lichen biota (Gowan and Brodo 1988; Arup 1994). The diversity in these habitats may exceed that in the intertidal zone. However, the composition and zonation of these communities remain little investigated. Along the north shore of the Bay of Fundy, rocks subject to salt spray and nutrient enrichment by guano are locally colonized by several disjunct halophilic arctic–boreal species. In the AME, these are at the southern limits of their overall ranges. They include, for example, Acarospora molybdina (Wahlenb.) Trevis., Lecanora contractula Nyl., and L. straminea (Wahlenb.) Ach. Lecanora orae-frigidae R. Sant. has a similar range, but occurs on driftwood.

Adventive species

Only Lecanora conizaedioes Nyl. ex Cremb., a toxitolerant species present in and near Halifax, Nova Scotia, and Saint John, New Brunswick (LaGrea and Stutzman 2006), is definitely known to be non-native in the AME. This species occurs widely in industrialized areas of western Europe, where it increased dramatically in abundance between the mid nineteenth and mid twentieth centuries in response to increasing sulphur dioxide air pollution. It was first noted in North America in 1956 in St. John’s, Newfoundland (Ahti 1965), but had likely become established there and in Halifax and Saint John before the 1950s.

Several other species are possibly non-native, and others with ruderal life histories have become more abundant, owing to the creation and maintenance of novel habitats by human activity. Among the former, Evernia prunastri (L.) Ach., Phaeophyscia orbicularis (Neck.) Moberg, and Xanthoparmelia mougeotii (Schaer.) Hale are candidates. Each of these species occurs only sporadically in the ecozone, and mainly in anthropogenic habitats. Evernia prunastri is locally frequent in forests of old-field origin along the north coast of Prince Edward Island, and scattered elsewhere in settled areas. Roadbanks are conspicuous examples of habitats conducive to the spread of ruderal species. Dibaeis baemoyces (L. f.) Rambold & Hertel is prominent among the latter, forming vast roadside populations on recently exposed, acidic mineral soil in the cooler, wetter portions of the ecozone.

The rarity of adventive lichens in the AME is as striking as the commonness of adventive seed plants (excluding gymnosperms). About 38% of the vascular flora of the ecozone consists of non-native species (Hill and Blaney 2010). There are no ferns or fern allies among these, nor are any of the bryophytes occurring in the ecozone known with certainty to be adventive. These disparities are not peculiar to the AME, but characteristic of angiosperm, versus pteridophyte, bryophyte, and lichen biotas throughout the northern hemisphere. They suggest that lichens and other cryptogams have occupied their potential global ranges more fully than have seed plants (see Otte et al. 2005). The greater uniformity of cryptogamic biotas around the northern hemisphere may be partly attributable to the greater antiquity of species in these groups. But the potential for dispersal of the smaller diaspores of lichens, bryophytes, and pteridophytes over much greater distances than the seeds of most angiosperms and gymnosperms is also likely to be implicated. European exploration and settlement of North America provided a vehicle for the introduction of many Old World vascular plants. It is possible that cryptic introductions of “alien” genotypes of lichen fungal and photobiont species have also occurred. If the latter species were already represented in the AME or North America by native genotypes, then the introductions are likely to be detectable only through intensive molecular phylogeographic studies.

A complementary problem of interest is the absence of some of the most common lichens of the AME and eastern North America from Europe. Among these are, for example, Buellia stillingiana, Cladonia cristatella Tuck., Lecanora hybocarpa (Tuck.) Brodo, Pertusaria macounii, Physcia millegranus Degel., Platismatia tuckermanii, Punctelia rudecta, Pyrrhospora varians (Ach.) R.C. Harris, Rinodina subminuta, and Ropalospora chlorantha. It seems very likely that propagules of these lichens occasionally reach Europe. Most of those noted lack joint fungal–algal diaspores, and could be limited by the unavailability of, or competition for, compatible photobionts. In any case, it can be postulated that their absence from Europe is due to as yet unknown biotic, climatic, or other ecological factors, rather than to dispersal limitations. A similar approach can be taken toward interpreting the distributions of species within the AME, and the absence of others.

Conclusions

This chapter has focussed on the diversity and distributions of the lichens of the AME in historical and bioclimatic contexts. While considerable gaps remain in knowledge of these subjects, other areas are equally in need of investigation. Among these are the community structure and composition, habitat and substrate ecology, life histories, and conservation of the lichen biota. Gowan and Brodo (1988) described the saxicolous, terricolous, corticolous, and lignonicolous communities in Fundy National Park. No comparable synopses have been attempted for other portions of the ecozone, and community structure has rarely been quantified (e.g., Cameron 2002). Habitats and communities known on the basis of general surveys to be species-rich in the AME include (but are not limited to): upland tolerant hardwood forests; mixed and hardwood swamp-forests, especially those with red maple or black ash (Fraxinus nigra Marsh.); coastal and other humid spruce–fir–birch forests; wet to mesic arborvitae forests; mixed forests on alluvial river terraces, including those with balsam poplar or aspen (Populus balsamifera L., P. tremuloides Michx.); high-elevation and other rocky heaths; peatlands; rocky lakeshores, rivershores, and seashores; and rocky talus slopes, cliffs, bluffs, ravines, and waterfalls.

Another area as yet little studied in the ecozone is the use of lichens for food, shelter, and camouflage by invertebrates. Li-
chens also provide nesting material for various small mammals and songbirds, mostly strikingly for the parula warbler (*Parula americana* (Linnaeus)), which models its nest entirely within living thalli of *Usnea*. Recently, it has been discovered that eastern pipistrelle bats (*Perimyotis subflavus* Cuvier) in Nova Scotia roost in massed *Usnea* thalli (Quinn and Broders 2007). Caribou formerly browsed lichens extensively in the ecozone (Clayden 1997), but with the exception of a small population persisting in the Chic-Choc Mountains, were extirpated here by the 1930s.

Owing to the scarcity of early collections and studies of lichens in the AME, it is rarely possible to draw direct conclusions about long-term population trends. Where the historical extent of a species’ habitat is known to have declined, it can be inferred, however, that there have been corresponding reductions in the abundance and distribution of that species. It is thus highly likely that lichens dependent on old-growth forest habitats have undergone, and continue to undergo, extensive declines and population fragmentation in the ecozone. For example, a recent study of *Lobaria* populations in tolerant hardwood forests in New Brunswick indicates that selective cutting on intervals of a few decades is not compatible with the maintenance of these and other old-growth-dependent species (Edman et al. 2008). Extending cutting cycles, retaining large trees as sources of propagules, and harvesting so as to emulate small-scale gap dynamics, may go some distance toward arresting declines of species in these communities. Above all, however, “there is an urgent need for conservation measures to be taken in this region to safeguard the last mature, closed-canopy deciduous forests” (Edman et al. 2008).

Many other examples of pressures on forest-inhabiting lichens in the AME could be given (see, for example, Richardson and Cameron 2004). In addition to the impacts of forestry, there are significant adverse effects on diversity resulting from air pollution, including acid rain and fog, and a wide range of land uses entailing habitat loss or alteration. But threatened habitats and species, population trends, and conservation priorities are subjects deserving of full treatment elsewhere. The importance of the ecozone as a modern refuge for lichen diversity in northeastern North America is highlighted by the losses and declines that have occurred in neighbouring regions. Of 467 species of macrolichens recorded historically in New England, 14.5% have not been observed or collected since 1950, and 56% are considered to be rare or declining (Hinds and Hinds 2008). Pollution-sensitive cyanolichens, and species restricted to mature forests are significantly over-represented among these. Comparable changes have occurred in southern Ontario (Wong and Brodo 1992). Many of the lichens that have disappeared, or that are rare and declining in these regions, are still present in the Atlantic Maritime Ecozone.

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Species Diversity in the Atlantic Maritime Ecozone


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